RESEARCH

Comparative Analysis of the Dorsal Chaetotaxy of *Troglopedetes*, *Trogolaphysa,* and *Campylothorax* Supports the Synonymization of Tribes Paronellini and Troglopedetini (Collembola: Paronellidae)

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ABSTRACT. Genera in subfamily Paronellinae have been grouped into five tribes, in part based on chaetotaxy. Tribes Bromacanthini, Paronellini, and Troglopedetini are characterized by having rounded scales and reduced or no macrochaetae, and although Bromacanthini harbors two well-differentiated genera, the core genera in tribes Paronellini and Troglopedetini form a homogeneous group where even generic diagnoses were, until recently, unclear. The genera assigned to Troglopedetini (*Troglopedetes* Absolon, *Trogolaphysa* Mills, and *Cyphoderopsis* Carpenter) harbor many species with reduced eyes number, whereas the tribe Paronellini (genera *Paronella* Schött, *Dicranocentruga* Wray and *Campylothorax* Schött) includes species with 6–8 eyes. Recent analyses of the chaetotaxy of *Trogolaphysa* and *Cyphoderopsis* suggest that these genera represent specialized forms related to species in Paronellini. The taxonomy of *Troglopedetes*, the type genus of Troglopedetini, is based almost exclusively on claw and mucro shape and dorsal macrochaetae pattern, and few details of the complete dorsal chaetotaxy of the species are known. This contribution presents a comparative analysis of the complete dorsal chaetotaxy of two species of *Troglopedetes* from Spain (one new to science), two new species of *Trogolaphysa* from the Dominican Republic and Martinique, and *Campylothorax sabanus* with the purpose of identifying aspects of the chaetotaxy that could provide diagnostic characters for the separation of *Trogolaphysa* and *Troglopedetes*, and a new diagnosis for tribe Troglopedetini. The analysis shows that neither the number of chaetae nor its organization or pattern of macrochaeta provides diagnostic differences between *Trogolaphysa* and *Troglopedetes*. It is also concluded that the separation of Paronellini and Troglopedetini is not justified. Troglopedetini is here synonymized with Paronellini, and a new diagnosis of Paronellini is provided.

Key Words: Spain, Dominican Republic, Martinique, *Cyphoderopsis*, entomobryoidea

The genus *Troglopedetes* Absolon comprises some 35 species distributed throughout the temperate and tropical regions of Eurasia (Bellinger et al. 1996–2013). Most temperate species are restricted to caves, but tropical forms are found both in caves and surface habitats (Deharveng 1987).

The relationship and taxonomic status of *Troglopedetes* with respect to similar genera (*Trogolaphysa* Mills, *Dicranocentruga* Wray, *Cyphoderopsis* Carpenter, *Trogonella* Delamare-Deboutteville, and *Troglopedetina* Delamare-Deboutteville) has been a source of controversy (Deharveng 1987, Mari Mutt 1987, Yoshii 1988). Thibaud and Najt (1988) reviewed a significant number of species assigned to the genera listed above and proposed new diagnoses for *Trogolaphysa*, *Troglopedetes,* and *Cyphoderopsis*, and the synonymization of *Dicranocentruga*, *Troglopedetina,* and *Trogonella*, under each of the firstly cited genera, respectively. Thibaud and Najt (1988) restricted *Troglopedetes* to species with fourth antennal segment subdivided, labial chaeta l_2 reduced, 0–3 eyes, and mucro relatively long, whereas *Trogolaphysa* grouped species with the fourth antennal segment undivided, labial chaetae L_2 normal, 0–8 eyes, and short mucro with 3–5 teeth. Mitra (1993) supported the separation of *Troglopedetes*, *Trogolaphysa*, *Cyphoderopsis,* and *Dicranocentruga* and placed the first three genera in the tribe Troglopedetini Börner, whereas *Dicranocentruga* was allocated to Paronellini Börner, based on the presence of the extra ocular structure (EOS; Mitra 1972). Mitra (2002) reiterated his placement of all species with 6+6 or more eyes and an EOS in *Dicranocentruga*.

Soto-Adames and Taylor (2013) studied the dorsal chaetotaxy of two species of *Trogolaphysa* and three species originally assigned to *Dicranocentruga* and, in agreement with Thibaud and Najt (1988), concluded that there are no differences in the organization of the chaetotaxy to justify the separation of the genera. The synonymization of *Dicranocentruga* and *Trogolaphysa* has further implications for classification. The genus *Trogolaphysa* was traditionally placed in tribe Troglopedetini, whereas *Dicranocentruga* was placed in Paronellini (Mitra 1993, 2002). The chaetotaxy organization reported by Soto-Adames and Taylor (2013) suggested *Trogolaphysa* should be placed in Paronellini. Likewise, recent work by Jantarit et al. (2013) shows that the idiochaetotaxy (i.e., all chaetae distinct from the basic chaeta; in the species under scrutiny, the basic chaetotaxy is formed by scales) of *Cyphoderopsis* does not differ in organization from that of *Trogolaphysa*. Transferring *Trogolaphysa* and *Cyphoderopsis* to Paronellini would leave tribe Troglopedetini harboring only the genus *Troglopedetes* and in need of a new diagnosis.

The taxonomy of *Troglopedetes* is based almost exclusively on claw shape and dorsal macrochaetae pattern (Deharveng and Gers 1993), and few other aspects of the morphology are included in species descriptions. As a result, most of the dorsal chaetotaxy *Troglopedetes* remains undescribed.

The purpose of this study is to determine whether dorsal chaetotaxy provides diagnostic characters for the separation of *Trogolaphysa* and *Troglopedetes*, and a new diagnosis for tribe Troglopedetini. This contribution presents a comparative analysis of the complete dorsal chaetotaxy of two species of *Troglopedetes* from Spain and two species of *Trogolaphysa* from the Dominican Republic and Martinique. The chaetotaxy of these four species, and the six species treated by Soto-Adames and Taylor (2013), is compared with the chaetotaxy of *Campylothorax sabanus* (Wray 1953), a member of tribe Paronellini. This study concludes that the dorsal chaetotaxy in *Trogolaphysa* and *Troglopedetes* is

similarly organized and does not provide additional diagnostic characters to separate the genera. Furthermore, the similarity in chaetotaxy organization in *Campylothorax, Trogolaphysa, Troglopedetes,* and *Cyphoderopsis* indicates that there is no justification for retaining tribe Troglopedetini, hence *Troglopedetes* and *Cyphoderopsis* are transferred to tribe Paronellini.

Materials and Methods

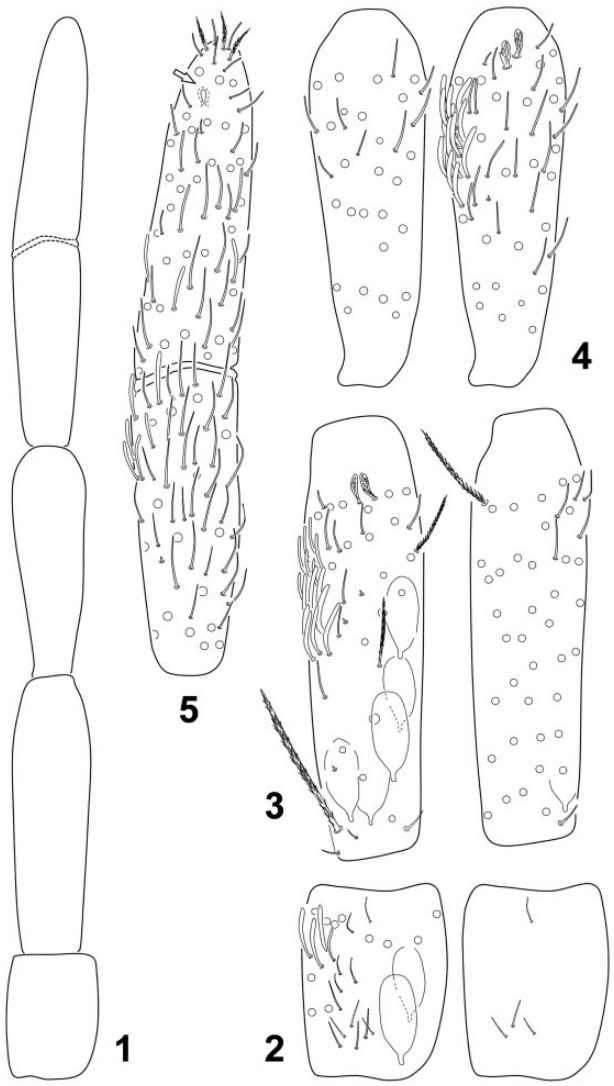
Selected specimens were cleared in Nesbitt's solution, mounted in Mark André II (Mari Mutt 1979) on glass slides, and examined under a compound microscope with phase-contrast. Drawings were made using a drawing tube, with final illustrations completed using Microsoft Power Point v14.3.5 Redmon, WA.

Throughout the descriptions, the abbreviations Ant., Th., and Abd. stand for antennal, thoracic, and abdominal segments, respectively. The formula for the labial chaetotaxy follows Christiansen and Bellinger (1998), where upper case represents macrochaetae, lower case microchaetae, underscore ciliate chaetae, and without underscore smooth chaetae. Repositories of material studied are the Illinois Natural History Survey at the University of Illinois, Champaign, IL (INHS); National Museum of Natural Sciences, Madrid, Spain (MNCN); National Museum of Natural History, Paris, France (MNHN); Natural Science Museum of Barcelona (MCNB); Museum of Zoology, University of Navarra, Pamplona, Spain (MZNA); and Carnegie Museum of Natural History, Pittsburgh, PA (CMNH).

Nomenclature of head and body chaetotaxy follow the systems of Jordana and Baquero (2005), Soto-Adames (2008, 2010), and Szeptycki (1979). The nomenclature of head chaetae is based on a combination of assumptions about which chaetae are primary (Barra 1975, Soto-Adames 2008, Pan et al. 2011) and their insertion relative to other chaetae and head landmarks (e.g., eye patch and dorsal sulcus). Head chaetae can be divided into anterior (series A, M, S, and Ps) and posterior (series Pa, Pm, and Pp). In the genera under consideration, most anterior head chaetae can be unambiguously identified following the model in Figs. 11 and 55. The only chaetae open to interpretation are those lateral to series A, which may be interpreted as either A_4 or A_5. Following Soto-Adames (2008) and Pan et al. (2011), A_5 is a primary macrochaeta, whereas A_4 is a secondary microchaeta, hence the external macrochaeta in *C. sabanus* is identified as A_5. Other chaetae associated to series A are unstable and were not identified. Posterior chaetae are often difficult to identify due to inadequacies of the mounting technique. Row Pa includes only four chaetae, which are identified as Pa_2, Pa_3, Pa_5, and Pa_6. Chaeta Pa_6 is always a trichobothrium, and Pa_5 is often transformed into a macrochaeta. The number of chaetae in rows Pm and Pp in adults is unclear, but one or two members of these rows are often modified into macrochaetae. The anterior macrochaeta was identified as Pm_3, as it is almost invariably inserted directly below Pa_3 or between Pa_2 and Pa_3, and the posterior one as Pp_3. Macrochaeta Pp_3 is common in *Troglopedetes* spp. (Deharveng 1988, 1990; Deharveng and Gers 1993), including the two species studied here.

Dorsal body chaetotaxy follows Szeptycki (1979), but chaeta identification is based on the relative position of each element in a general model with a full complement of chaetae. The idiochaetotaxy of the species considered here is reduced in comparison with other scaled Entomobryoidea and identification of many elements is subjective. The criteria used to identify chaeta of unclear homology are discussed below.

Mesothorax. The anterior chaetae associated with the pseudopore belong to series m_2. In most species, there is a single chaeta displaced externally to the pseudopore, which is identified as m_{2e}. A chaetae is identified as m_2 only when inserted directly or almost directly above the pseudopore; the chaeta internal and near to the pseudopore is m_{2i}, whereas the element internal to the pseudopore, but closer to the collar than the pseudopore is m_1. Among species with known chaetotaxy, only *Trogolaphysa jacobyi* Soto-Adames and Taylor 2013 has more than one chaeta in series m_2, and under the present interpretation they were identified as m_2 and m_{2i}

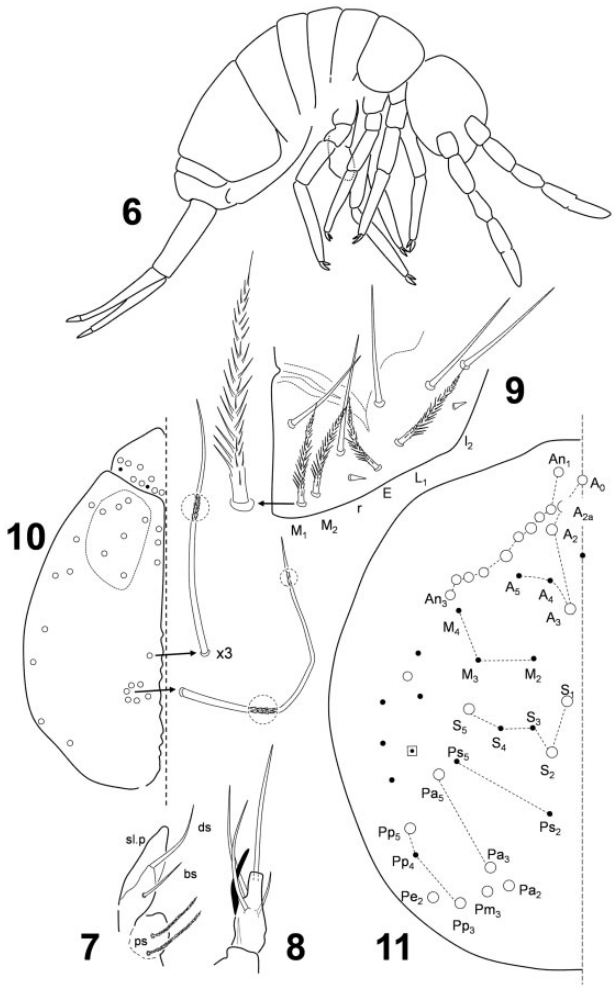


Figs. 1–5. *Troglopedetes absoloni*. (1) Complete antenna. (2) First antennal segment, left dorsal, right ventral. (3) Second antennal segment, left dorsal, right ventral. (4) Third antennal segment, left dorsal, right ventral. (5) Dorsal view of fourth antennal segment (the arrow points subapical organite).

First Abdominal Segment Chaeta p_6. The insertion of the latero-posterior chaeta on this segment appears to shifts from left to right and back in interspecific comparisons. The identification of the lateral chaetae as p_6 is based on the observation that when a_6 is present, the two chaetae are aligned.

Third Abdominal Segment. The chaetotaxy of the lateral trichobothrial complexes is difficult to homologize with the chaetotaxy of Entomobryidae. Several possible interpretations of the lateral chaetotaxy were explored, but in the absence of clear and strong evidence to support any of them, it was decided to adopt the interpretation presented in Fig. 22.

Fourth Abdominal Segment. Determination of the identity of chaetae in columns A and B is problematic because of pervasive anterior, posterior and lateral displacement of the elements in interspecific comparisons. To achieve a degree of objectivity, the system of Jordana and Baquero (2005) and Jordana (2012) was adopted, which divides the inner section of the segment into five (four in *Troglopedetes* and *Trogolaphysa*) zones delimited by more or less stable landmarks. In summary (Figs. 22 and 56), zones 6–7 are the fields above the anterior trichobothrium; zone 8 is the field between the anterior and medial trichobothria; zone 9 is the area



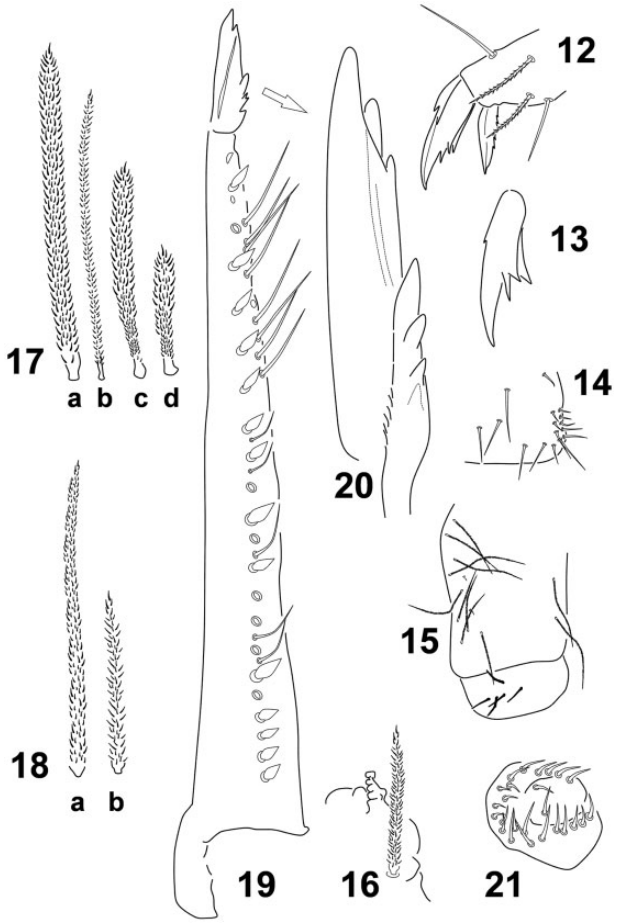
Figs. 6–11. *Troglopedetes absoloni*. Unless otherwise indicated: open circles, macrochaetae; close circles, microchaetae; open squares with dot, bothriotricha. (6) Habitus. (7) Pleural setae and setae of outer maxillary lobe; bs, basal seta; ds, distal seta; ps, pleural setae; sl. p, sublobular plate. (8) Chaetotaxy of labial palp Papilla E. (9) Labial triangle. (10) Ventral chaetotaxy of head, open and black circles are ciliate and smooth setae, respectively. (11) Dorsal chaetotaxy of head.

between the posterior trichobothrium and a line running from the pseudopore to chaeta T6; and zone 10 is the area below the pseudopore and T6. Chaetae in columns A–B inserted in zones 6–7 belong to row 3; chaetae in zone 8 are part of row 4; in zone 9 one finds rows 4–5, whereas zone 10 includes row 6, sometimes row 5, and more rarely row 4. Chaetae in column A inserted in zone 10 are called A_6, A_{i2}, or Ae_7 depending of their relative insertion: A_6 is inserted close to the posterior margin of the segment, at the same level as B_6, which is almost always present; chaeta Ai_2 is inserted anterior to B_6 and somewhat internal to the pseudopore (Figs. 38 and 45); Ae_7 is anterior to Ai_2 and inserted between columns A and B. The most posterior chaeta in column B was interpreted as B_{6p}, and the chaeta anterior to that as B_6.

Results

Species Level Diagnostic Characters in *Troglopedetes* and *Trogolaphysa*. A list of characters used to diagnose species of *Troglopedetes* and *Trogolaphysa* is presented below. Characters are divided in two groups: primary characters are considered sufficient by themselves, or in combination with one other character, to diagnose species; secondary characters are those that provide support for interspecific discontinuities suggested by primary characters but that by themselves are not thought of as providing sufficient evidence of population isolation. Primary characters typically are easy to observe, discrete, and show very little intrapopulation variation. Secondary characters may be difficult to observe consistently across a number of slide-mounted specimens, show continuous variation, or show varying levels of intrapopulation variation in different species. Characters considered secondary may prove to be, after analysis of a larger sample of species, as useful in species delimitation and identification as primary characters. It is recommended that at a minimum, all primary characters be described and illustrated for all species. However, a proper species description should provide information for all the characters listed below, irrespective of whether they are listed as primary or secondary. Characters below are listed in morphological order from anterior to posterior. Characters considered primary are followed by (P), whereas secondary characters are identified by (S).

1. Scale distribution (S)—The distribution of scales in these two genera is of little diagnostic utility. All species have distally rounded scales (Fig. 34) present on Ant. I–II, head, body, and ventral face of furcula. A few species have basal scales on the dorsal face of Ant. III, but these scales often fall off and evidence of their presence is not always clear.
2. Relative length of antennae to head length (S)—The head length is measured from the cervix to the interantennal area.
3. Subapical sense organ Ant. IV (S)—Typically, there is a short capitate or rod-like sensillum inserted in a shallow pit (Fig. 5), accompanied by a guard sensillum. The capitate sensillum seems to be always present, but in some species, like *Trogolaphysa sauron* n. sp., it is small and translucent, and it may appear to be absent. The guard chaeta is always present and rather conspicuous. Most of the unambiguous interspecific variation is found in the shape, relative size, and thickness of the guard sensillum.
4. Subdivision of Ant. IV (P)—The presence of a subdivision on Ant. IV (Fig. 5) distinguishes *Troglopedetes* from *Trogolaphysa*. Unfortunately, the fourth antennomere is often lost in cave forms with long antennae that are collected in pitfall traps or those that have to be dragged out of caves through narrow passages.
5. Sense organ of Ant. III (S)—Sensilla 2–3 (sensu Chen and Christiansen 1993) are, in general, rod-like in surface species and flat and laterally expanded in cave forms. Some species (Figs. 4 and 26) have additional distal sensilla on Ant. II.
6. Eye number (P)—The number varies from 0 to 8. This character is considered primary, but it should be noticed that eyes G and H are always reduced, sometimes to such extent that even when present they are difficult to see in regular mounts, and species with eight eyes are reported as having only six eyes. For this reason, eye number is good diagnostic character when fewer than six are present. Another caveat is that in large species with reduced number of eyes (e.g., *T. jacobyi*), the EOS is large enough to be confused with an eye. The EOS is typically found between chaetae Ps_5 and Pa_5 (Figs. 39 and 60), and any eye-like structure observed in this area should be tentatively reported as EOS, until examination under polarized light or SEM can be arranged.
7. Number of chaetae in eye valley (S)—The number of chaetae in the eye valley varies from 3 to 6. This character can be scored only when eyes E and F are present. This character is stable and useful to distinguish *Trogolaphysa jataca* (Wray 1953) from *Trogolaphysa geminata* (Mari Mutt 1987), but many more species need to be evaluated before it can be considered primary.
8. Number of chaetae along the dorsal base of the antennae (S)—The row of chaetae along the dorsal base of the antennae, denominated An, includes macro- and mesochaetae with large sockets. The number chaetae shows instraspecific variation related to post-embryonic development, but the range of chaetae in adults can be used to separate groups of species.
9. Dorsal head chaetotaxy (P)—Most species level variation is found in the number of macrochaetae in series A, M, and S. The two



Figs. 12–21. *Troglopedetes absoloni*. (12) Metathoracic claw complex. (13) Detail of metathoracic unguis from a different individual. (14) Trochanteral organ. (15) Lateral view of ventral tube, anterior face is to the right. (16) Tenaculum. (17) Representative chaetae of dens, chaetae a and b are present only on distal end of dens. (18) Representative manubrial chaetae. (19) Dens and mucro. (20) Detail of mucro. (21) Male genital plate.

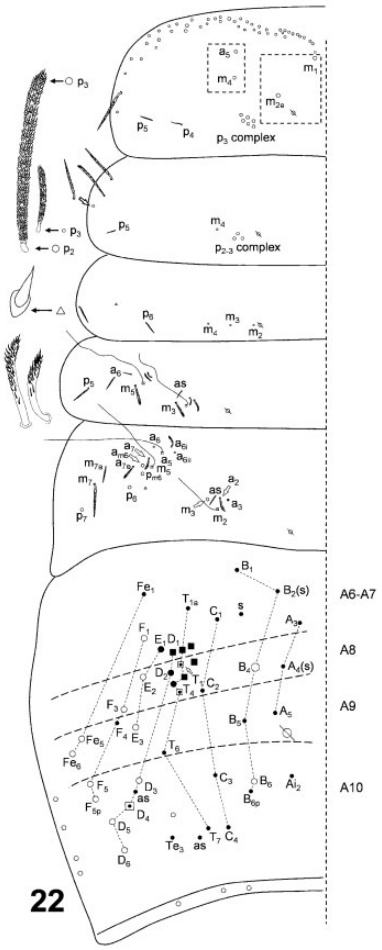
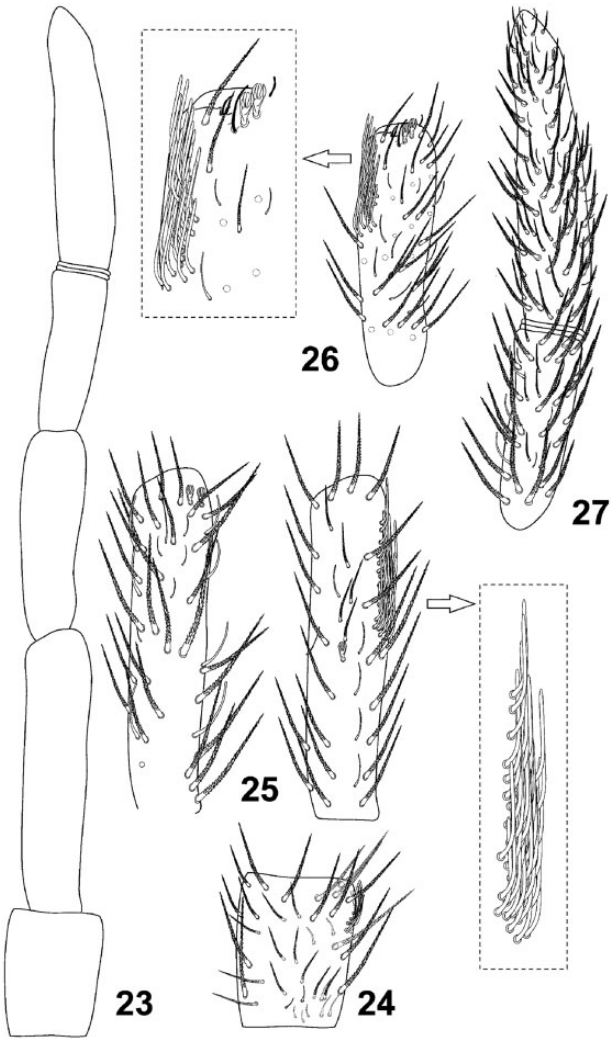


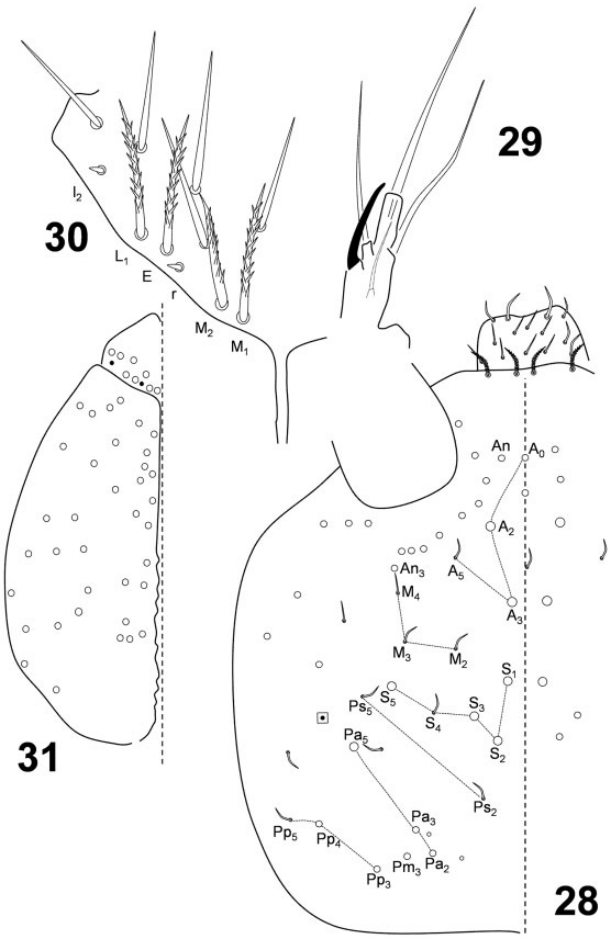
Fig. 22. *Troglopedetes absoloni*. Complete dorsal chaetotaxy of body. Open circles, macrochaetae; close circles, microchaetae; open squares with dot, bothriotricha; black squares, fan-shaped setae; open circles with cross bar, pseudopores.

most common posterior macrochaeta are Pa_5, Pm_3, and, in *Troglopedetes*, Pp_3.

10. Prelabral chaetae ornamentation (P)—All species have four prelabral chaetae. Most species have ciliate prelabral chaetae, but in *T. jacobyi* and a few other species, the chaetae are smooth. This character seems to be very stable within species, but it is often left out of species descriptions.
11. Labral chaetae (S)—All species have 554 chaetae on the basal (A), medial (B), and distal (C) rows, respectively (Ojeda and Palacios-Vargas 1983). There is species-specific variation in the relative size of chaetae in row B. In some species, all chaetae in row B are subequal to each other but ostensibly more delicate than chaetae in rows A and C. Other species show differences in the size among elements in row B, usually chaetae B_2 are shorter than B_0 and B_1. This character is often difficult to score, unless the labrum lays flat on the preparation.
12. Ornamentation of labral margin (P)—The distal margin of the labrum may bear 1+1 spine-like projections or it may be smooth. The spines may be completely separated or may show different levels of basal fusion, such that they may look Y-shaped.
13. Number of appendages on the sublobal plate of the maxillary palp (S)—The number of appendages is usually 2, but some species have a smooth plate. This character is also very stable within species, but it is often difficult to score.
14. Labial chaetae (P)—The number of posterior chaetae is $M_1M_2r(R)EL_1L_2(l_2)$, but the ornamentation is informative for species identification. In some species, all chaetae, except r, are ciliate, whereas in others, the chaetae are smooth. In addition, L_2 can be a ciliate macrochaeta or smooth microchaeta.
15. Number of chaetae along ventral head groove and postlabial scales (P)—Most species have a uniform cover of scales on the postlabial area, there are few postlabial chaetae, and up to 4+4 chaetae along the ventral groove. In species with few or no postlabial scales, the area is polychaetotic, and the number of chaetae along the groove is greater than 4+4. In almost all species, the posterior chaeta along the ventral groove is inserted far away from the anterior chaetae.
16. Dorsal macrochaeta of body (P)—All interspecific variation in the number of macrochaetae in the species evaluated is limited to the Th. II–III and the inner columns of the Abd IV. The lateral macrochaetae of Abd. IV are of limited diagnostic utility, as the stable chaetae (anterior elements in series D–F) are almost invariant, and the externo-posterior macrochaetae appear to vary according to size or instar of the individual. The chaetae (including macrochaetae) on Abd. II–III show little to no variation between species. The possible exceptions are some chaetae lateral to the trichobothrial complexes, but these chaetae are difficult to score consistently across individuals.
17. Relative position of lateral sensillum and microsensillum on Th II (S)—In most *Trogolaphysa,* the lateral sensillum is inserted



Figs. 23–27. *Troglopedetes ildumensis* n. sp. (23) Complete antenna. (24) Dorsal chaetotaxy of first antennal segment. (25) Second antennal segment, left dorsal, right ventral. (26) Dorsal chaetotaxy of third antennal segment. (27) Dorsal chaetotaxy of fourth antennal segment.



Figs. 28–31. *Troglopedetes ildumensis* n. sp. (28) Dorsal chaetotaxy of head, open circles, macrochaetae; close circles, microchaetae; open squares with dot, bothriotricha. (29) Chaetotaxy of labial palp Papilla E. (30) Labial triangle. (31) Ventral chaetotaxy of head.

anterior to the microsensillum, but in *Trogolaphysa belizeana* Palacios-Vargas and Thibaud and *T. jacobyi*, the microsensillum is anterior and the sensillum posterior. This character has not been described for most species, and its diagnostic utility beyond the two species mentioned above is unclear.

18. Presence or absence of chaeta a_6 on Abd I (S): This chaeta may be present or absent. There is some intraspecific variation in some species, but the presence or absence of the chaeta is stable in most species examined.
19. Number of posterior chaetae of Abd IV (S)—These chaetae are variable and informative. In the *Trogolaphysa* examined, species have either 7 or up to 13–15 per side.
20. Trochanteral organ (S)—This is a continuous character, and unless the legs are properly and cleanly dissected, the actual number of spines is often difficult to ascertain.
21. Claw complex (P)—This is one of the most important character systems used to diagnose species in *Trogolaphysa* and *Troglopedetes*. The claw complex show interspecific variation in the shape of the tenent hair, shape, and number of teeth on the unguiculus, and number, shape, and distribution of teeth on the unguis. Describing the shape of the teeth is often challenging, and an illustration of the claw should always be included with descriptions.
22. Number of distal macrochaetae on anterior face of collophore (S)—These macrochaetae are relatively easy to observe, but smaller or younger individuals have fewer macrochaetae than larger adults.
23. Dens spines (S)—The number of rows of spines on the dens is either 1 or 2 depending on the species; in *Troglopedetes,* there is a single row, whereas in most *Trogolaphysa* species there are two rows of spines. The number of spines and their ornamentation is often reported and may be useful to delimit species, but this number varies intraspecifically with specimen size, and the ornamentation appears to vary from smooth to ciliate within individuals along the length of the dens.
24. Mucro (P)—The number of teeth and relative length of the mucro are usually species specific, although in some species both characters show intraspecific variation. The relative length of the mucro is sometimes expressed as a proportion of the length of the dens, but many older descriptions do not report this proportion. Most old descriptions provide figures of the mucro, from which we can derive the relative length of the mucro as the ratio of its length to its width (measured at the juncture with the dens). Using this measure, *Trogolaphysa* has a relatively short and wide mucro, whereas in *Troglopedetes,* the mucro is long and narrow. Mucronal teeth have different general distribution in *Trogolaphysa* and *Troglopedetes*. *Trogolaphysa* typically have

Table 1. Diagnostic characters for species of *Trogolaphysa* and *Troglopedetes* described here and *Campylothorax sabanus*

	T. quisqueyana n. sp.	*T. sauron* n. sp.	*Trogl. absoloni*	*Trogl. ildumensis* n. sp.	*C. sabanus*
Eye number	8	8	0	0	8
Ant. 4 subsegment	No	No	Yes	Yes	No
Anterior head macrochaetae	5	3	5	6	8
Head chaetae A_0	Macrochaeta	Macrochaeta	Macrochaeta	Macrochaeta	Macrochaeta
Head chaetae A_2	Macrochaeta	Macrochaeta	Macrochaeta	Macrochaeta	Macrochaeta
Head chaetae A_3	Macrochaeta	Microchaeta	Macrochaeta	Macrochaeta	Macrochaeta
Head chaetae A_5	Absent	Absent	Microchaeta	Microchaeta	Macrochaeta
Head chaetae M_2	Macrochaeta	Macrochaeta	Microchaeta	Microchaeta	Absent
Head chaetae M_3	Microchaeta	Microchaeta	Microchaeta	Microchaeta	Absent
Head chaetae S_2	Microchaeta	Microchaeta	Macrochaeta	Macrochaeta	Macrochaeta
Head chaetae S_3	Macrochaeta	Microchaeta	Microchaeta	Macrochaeta	Macrochaeta
Head chaetae S_4	Microchaeta	Microchaeta	Microchaeta	Microchaeta	Macrochaeta
Head chaeta S_{5i}	Absent	Absent	Absent	Absent	Microchaeta
Head chaetae S_5	Macrochaeta	Microchaeta	Macrochaeta	Macrochaeta	Macrochaeta
Posterior head macrochaetae	2	1	7	6	1
Head chaetae Pa_5	Macrochaeta	Macrochaeta	Macrochaeta	Macrochaeta	Macrochaeta
Head chaetae Pm_3	Macrochaeta	Microchaeta	Macrochaeta	Macrochaeta	absent
Prelabral setae	Ciliate	Ciliate	Ciliate	Ciliate	Ciliate
Distal margin labrum	1+1 hooks	1+1 hooks	Smooth	Smooth	Smooth
Labium M_1	Ciliate macrochaeta	Ciliate macrochaeta	Ciliate macrochaeta	Ciliate macrochaeta	Ciliate macrochaeta
Labium M_2	Ciliate macrochaeta	Ciliate macrochaeta	Ciliate macrochaeta	Ciliate macrochaeta	Ciliate macrochaeta
Labium r	Smooth microchaeta	Smooth microchaeta	Smooth microchaeta	Smooth microchaeta	Smooth macrochaeta
Labium E	Ciliate macrochaeta	Ciliate macrochaeta	Ciliate macrochaeta	Ciliate macrochaeta	Smooth macrochaeta
Labium L_1	Ciliate macrochaeta	Ciliate macrochaeta	Ciliate macrochaeta	Ciliate macrochaeta	Smooth macrochaeta
Labium L_2	Ciliate macrochaeta	Ciliate macrochaeta	Smooth microchaeta	Smooth microchaeta	Smooth microchaeta
Setae postlabial column I	4	4	4	6	5
Anterior macrochaetae Th. 2	1	1	2	2	0
Posterior macrochaetae Th. 2	6	3	6	6	7-8
Macrochaetae Th. 3	0	0	3–4	4	4
Inner macrochaetae Abd. 4	4	3	2	2	6
Tenent hair	Spatulate	Spatulate	Acuminate	Spatulate	Spatulate
Unguis inner teeth number	4	4	3	3	3
Unguis size paired teeth	Subequal	One thinner and longer	Subequal	One slightly larger	Subequal
Unguis paired teeth ending	Basal half	Near middle of unguis	Basal half	Basal half	Basal half
Unguis basal unpaired tooth ending	Distal half	Distal half	Distal half	Basal half	Distal half
Unguiculus shape	Lanceolate	Truncate	Lanceolate	Lanceolate	Truncate
Unguiculus ornamentation posterior lamella	Smooth	Serrate	Serrate	Serrate	Serrate
Number rows spine dens	2	2	1	1	2
Number teeth mucro	4	4	2-4 basal 3 distal	2 basal 3 distal	5

3–5 teeth, more or less equally distributed along the length of the mucro, but in *Troglopedetes,* there are 2–11 teeth forming basal and distal groups.

Species Description. Genus *Troglopedetes* Absolon, 1907, sensu Thibaud and Najt, 1988

Type species *Troglopedetes pallidus* Absolon, 1907

Scales present on Ant I–II, head, body, and ventral face of furcula; Ant IV subdivided; eyes 0–3; labial setae l2 reduced to a cone; dens with a single row of spines; mucro elongate, with distinct groups of basal and distal teeth.

Troglopedetes absoloni Bonet, 1931

(Figs. 1–22, Table 1)

Type Material. Holotype, slide labeled as "*Troglopedetes absoloni* Bonet 1931; 554N Mina del Capellat, Calpe. Tipo. 29.VIII.1930. F. Bonet; Cat. MNCN Cat. Tipos 9775; MNCN Ent No. Cat. 61163"; locality: Calpe (Alicante), Spain; deposited at MNCN (Madrid, Spain).

Additional Material. Spain: Cueva de la Fájara (Canillas de Aceituno, Sierra de Tejeda, Málaga): sample no. 3 (28.IX.2009), 7 specimens in ethanol; sample no. 4 (28.IX.2009), 5 specimens in ethanol; sample no. 5 (06.IX.2009), 15 specimens slide mounted; sample no. 5 (28.IX.2009), 1 specimen slide mounted; sample no. 9 (06.IX.2009), 3 specimens in ethanol; sample no. 11 (06.IX.2009), 2 specimens slide mounted; sample no. 15 (28.IX.2009), 15 specimens in ethanol; sample 142, 1 specimen slide mounted and 16 in ethanol (28.IX.2009); all samples GES-SEM leg. Cueva del Far: sample 2011 08 FT51; A. Sendra leg. All material deposited in MZNA (Pamplona, Spain).

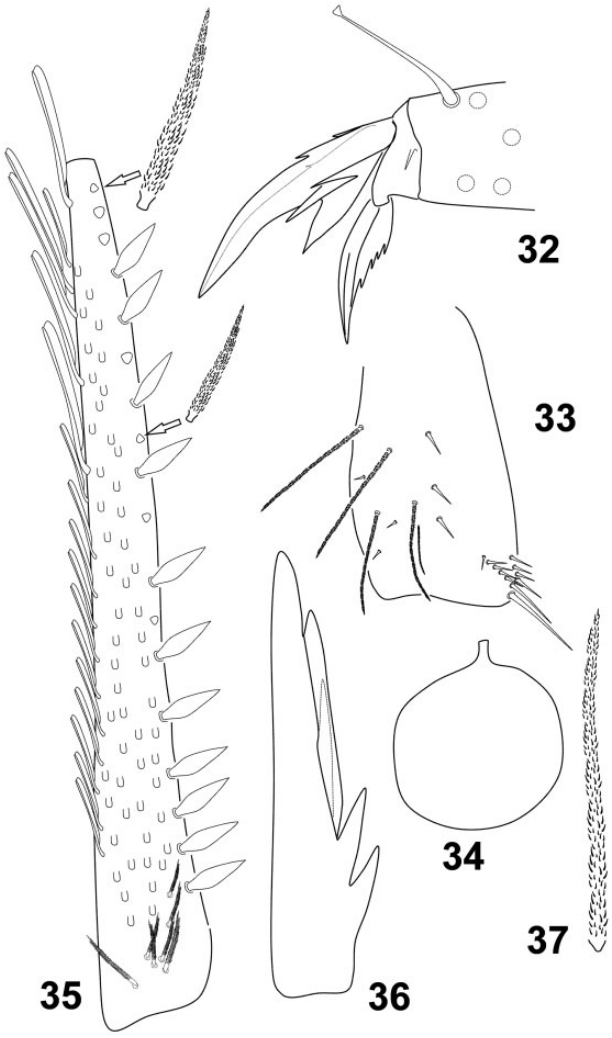
Distribution. In addition to the type locality, the species has been reported from eastern reaches of the Prebetico (Jaen and Alicante), la Cova de les Ratetes in the Serra de Corbera (Valencia), and Cova de les Meravelles de Llombai, this last one at the northeastern edge of the Plataforma del Caroig (Valencia) (Gamma 2005). This work extends the distribution of this species between the provinces of Malaga and Cordoba.

Size. 1.0–1.8 mm ($n = 18$); holotype 1.6 mm.

Color Pattern. White, without trace of pigment (Fig. 6).

Scale Distribution. Ant. I–II, head, body, and ventral face of furcula.

Head. Antennae 0.45× as long as body. Ant IV subdivided into two subsegments, without apical bulb, chaetae not forming whorls. Length antennal segments I–IVab as 50 µm, 130 µm, 140 µm, 104 µm, and 116 µm, respectively. Number of clubbed sensilla on antennal segments: 3–5 on Ant I, 15 on Ant II, 15 on Ant III, and 3–6 on distal area on Ant IVa (Figs. 1–5). Eyes absent. Head dorsally (Fig. 11) with six anterior (A_0, A_2, A_3, S_1, S_2, and S_5) and seven posterior (Pa_2, Pa_3, Pa_5, Pm_3, Pm_5, Pp_3, and Pe_2) macrochaetae; chaetae A_{2a} enlarged. Prelabral chaetae ciliate; labral chaetae smooth; distal margin of labrum smooth. Maxillary palp with subapical and papillate apical chaetae smooth; sublobal plate with two appendages (Fig. 7). Lateral appendage of labial papilla E as in Fig. 8. Labial triangle (Fig. 9) with $\underline{M_1M_2}r\underline{EL_1}l_2A_{1-5}$: M_1, M_2, E, and L_1 ciliate and subequal; r and l_2 short and smooth. All postlabial chaetae ciliate (Fig. 10), column I with four chaetae; with seven chaetae between columns I and O (group bound by hatched line in Fig. 10); ventral cervical chaetae 6–7 + 6–7.



Figs. 32–37. *Troglopedetes ildumensis* n. sp. (32) Metathoracic leg claw complex. (33) Trochanteral organ. (34) Scale typically found on posterior margin of third abdominal segment. (35) Dorsal view of dens. (36) Mucro. (37) Manubrial seta.

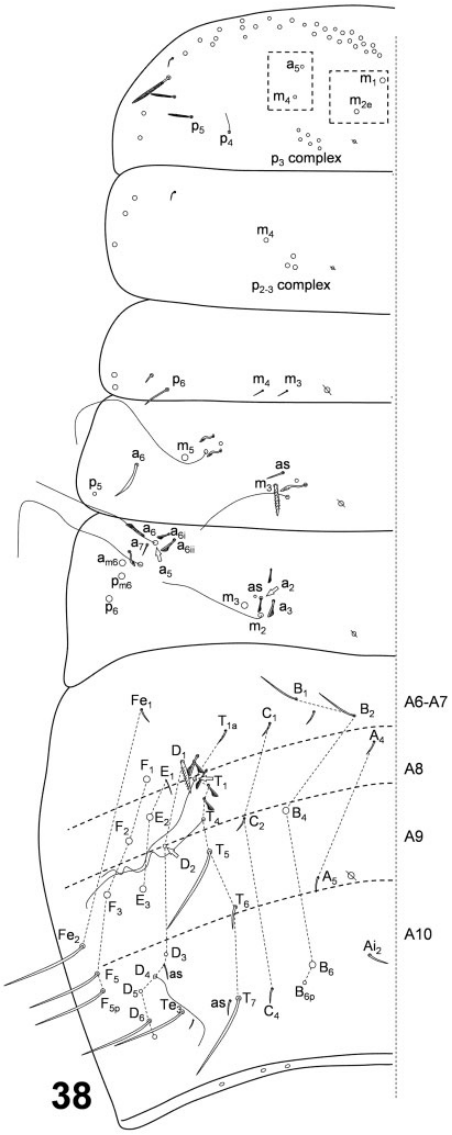


Fig. 38. *Troglopedetes ildumensis* n. sp. Dorsal chaetotaxy of body. Symbols as in Fig. 22.

Body. Dorsal body chaetotaxy as in Fig. 22. Th. II with four anterior (m_1, a_5, m_{2e}, and m_4) and six posterior (p_3 complex) macrochaetae. Th. III with four macrochaetae (a_2, p_2, p_3, and m_4). Abd. I chaeta a_6 absent, with four posterior microchetae, probably homologous to m_2, m_3, m_4, and p_6. Abd. II with four ciliate chaetae, two macrochaetae (m_3 and m_5), and one sensillum associated with macrochaeta m_3. Abd. III with four macrochaetae (m_3, am_6, pm_6, and p_6); chaetae associated with trichobothria smooth or distally ciliate: trichobothrium a_2 with two anterior, ciliate chaetae, trichobothrium a_5 with one smooth and one ciliate anterior chaetae, trichobothrium m5 with one anterior ciliate seta; sensilla as and d_2 present; five additional ciliate chaetae external to lateral trichobothrial complex arranged as in Fig. 22. Abd. IV with two inner macrochaetae (B_4, zone 8 and B_6, zone 10) and mesochaeta B_{6p}; large lateral macrochaetae correspond to D_3, E_2, E_3, F_1, F_2, and F_3; small lateral macrochaetae as in Fig. 22; lenticular organs rounded, present (3 + 3) in all specimens examined; posterior chaetae absent.

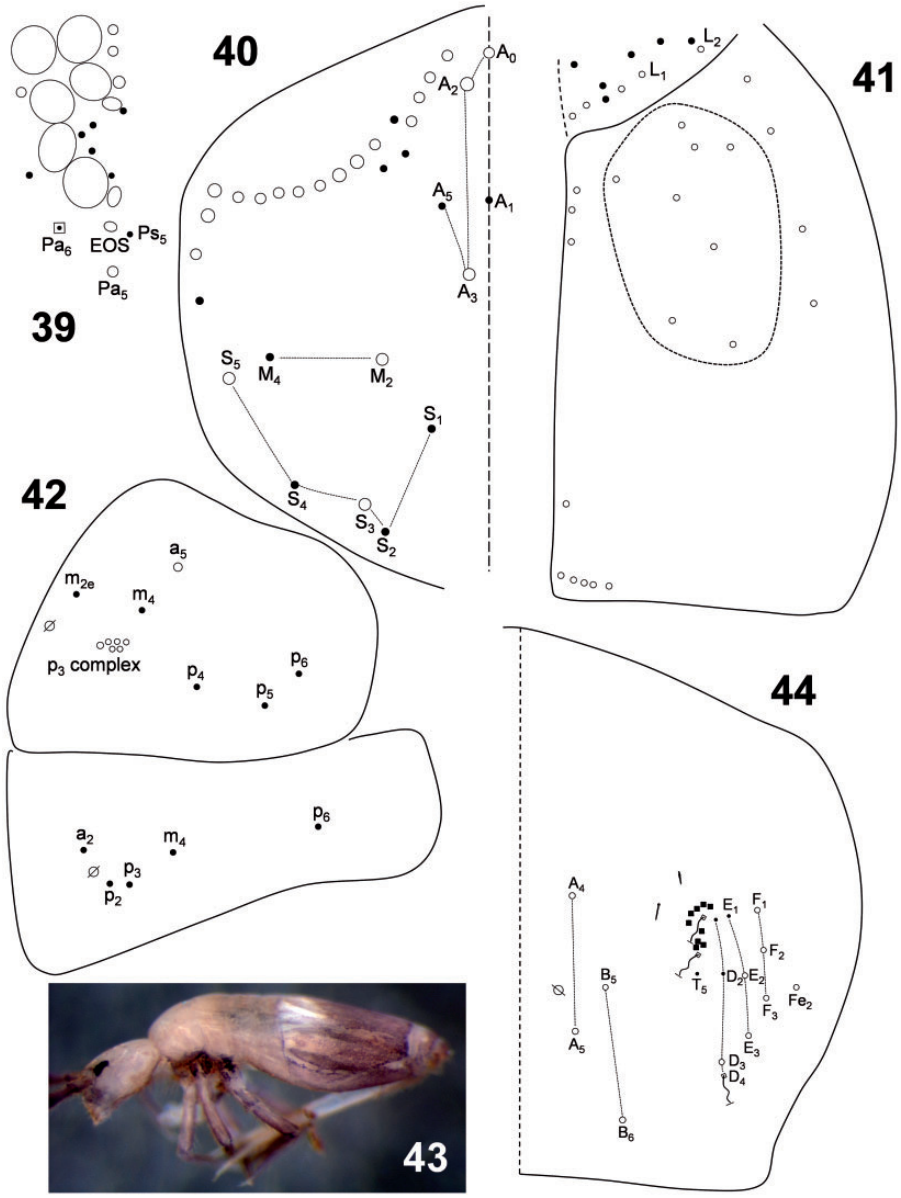
Male Genital Plate. Circinate, without modified chaetae (Fig. 21).

Legs. Trochanteral organ (Fig. 14) with 5–6 medium and 10–11 small, smooth straight chaetae, arranged in "V," distal chaeta largest. Metathoracic claw complex as in Figs. 12 and 13. Tenent hair acuminate or weakly spatulate (as in holotype), 0.8–0.9 times as long as claw. Unguis thick, with 3–4 inner teeth; paired internal teeth at 55–60% (proximal wings); proximal unpaired tooth at 65–70% inner ungual edge; distal unpaired tooth, when present (as in holotype, and in one leg of one specimen from Malaga), at 75% of inner ungual edge; one external tooth at 25–30%, and lateral teeth at 30% from claw base. Unguiculus lanceolate, with outer margin serrated.

Ventral Tube. Anterior face with 2+2 distal macrochaetae (Fig. 15). Lateral flaps with 5 + 5 chaetae (distal chaetae three smooth and one ciliate, all proximal chaeta ciliate). Posterior face with 9 + 9 long, coarsely ciliate chaetae, and 2 + 2 small spines at posterior area.

Tenaculum. Basally with a single coarsely ciliate chaeta; rami with four teeth (Fig. 16)

Furcula. Proportion manubrium:dens:mucro length = 1:0.85:0.14 (n = 3) (450 µm, 320 µm, and 50 µm, respectively, in holotype). Dorsal face of manubrium with many ciliate chaetae (Fig. 18). Dens (Fig. 19) slightly tapering, with 1 dorsal row of 16–22 smooth, stout spines, and intercalated chaetae following the pattern: $5–11/_{1–2}/1/_1/1/_1/1/_1/1/_1/1/_1/\ldots 1–2$, with a maximum of 22 spines (chaetae in subscript) (22 in holotype), and 2 external rows of chaetae 3× as long as spines (Fig. 17). Mucro (Fig. 20) stout, basally with 1 large and 2–4 small teeth, sometimes accompanied by minute lateral basal serrations; distally with 3 blunt teeth.



Figs. 39–44. *Trogolaphysa quisqueyana* n. sp. Unless otherwise indicated: open circles, macrochaetae; close circles, microchaetae; open squares with dot, bothriotricha; black squares, fan-shaped setae; open circles with cross bar, pseudopores. (39) Eye patch. (40) Dorsal chaetotaxy of head. (41) Ventral chaetotaxy of head, open and black circles are ciliate and smooth setae, respectively. (42) Dorsal chaetotaxy of thorax. (43) Habitus and color pattern. (44) Fourth abdominal segment dorsal macrochaetae.

Remarks. The small differences observed between the specimens from Valencia and Malaga do not justify the recognition of a different species. The group of blind *Troglolopedetes* comprises 26 species, of which 13 have a single row of dental spines. This group is further reduced to seven species, if only species having more than three basal mucronal teeth are considered. Among the seven species with more than three basal mucronal teeth, three have three distal teeth: *Trogl. absoloni*, *Troglopedetes machadoi* Delamare-Deboutteville 1946 (Portugal) and *Troglopedetes orientalis* Cassagnau and Delamare-Deboutteville 1955 (Lebanon). The unguiculus of *Trogl. absoloni* is externally serrate, whereas in the other two species, it is smooth. In addition, *Trogl. orientalis* carries 27–30 dental spines.

Troglopedetes ildumensis Soto-Adames, Jordana and Baquero n. sp. (Figs. 23–38, Table 1)

Etymology. The name of the species refers to Ildum, the original roman name for the municipality of Cabanes, near where the cave in which the new species was collected is located,

Type locality. Spain: L'avenç del Mas de la Cova, Cabanes (Castellón). Coordinates (ED 50): 31T0251173/4445105, (GSW84: N 40.11951 E 0.08001), 304 m.

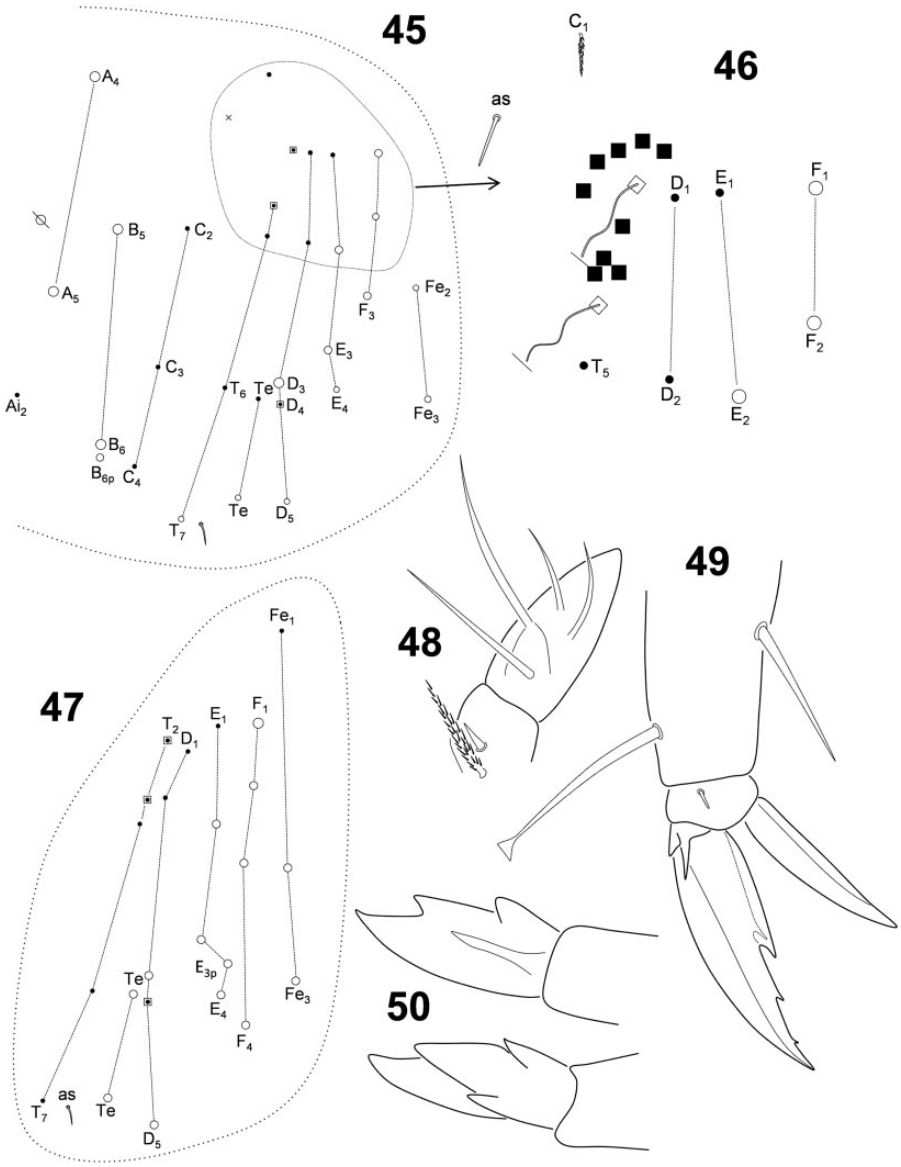
Material Examined. Spain: Holotype, one female on slide, 27.XII.2011, code Ta-1-13-3(2); two paratypes on slides, codes Ta-1-13-3(1) and Ta-1-13-3(3); and 21 paratypes in ethanol, sample Ta-1-13-3; F. Fadrique leg. All specimens, except for two paratypes deposited in the MCNB (Barcelona, Spain), are deposited in MZNA (Pamplona, Spain).

Size. 1.1–1.5 mm.

Color Pattern. White, without trace of pigment.

Scale Distribution. Ant. I, head, body, and ventral face of furcula.

Head. Antennae 0.42× as long as body. Ant IV subdivided into two subsegments (Figs. 23 and 27), without apical bulb, chaetae not forming whorls. Length Ant. I–IVab (Fig. 23) as 80 µm, 170 µm, 130 µm, 110 µm, and 150 µm, respectively, total 640 µm (holotype). Ant. I–III with 2–5, 25–30, and 25–30 blunt sensilla, respectively (Figs. 24–26).

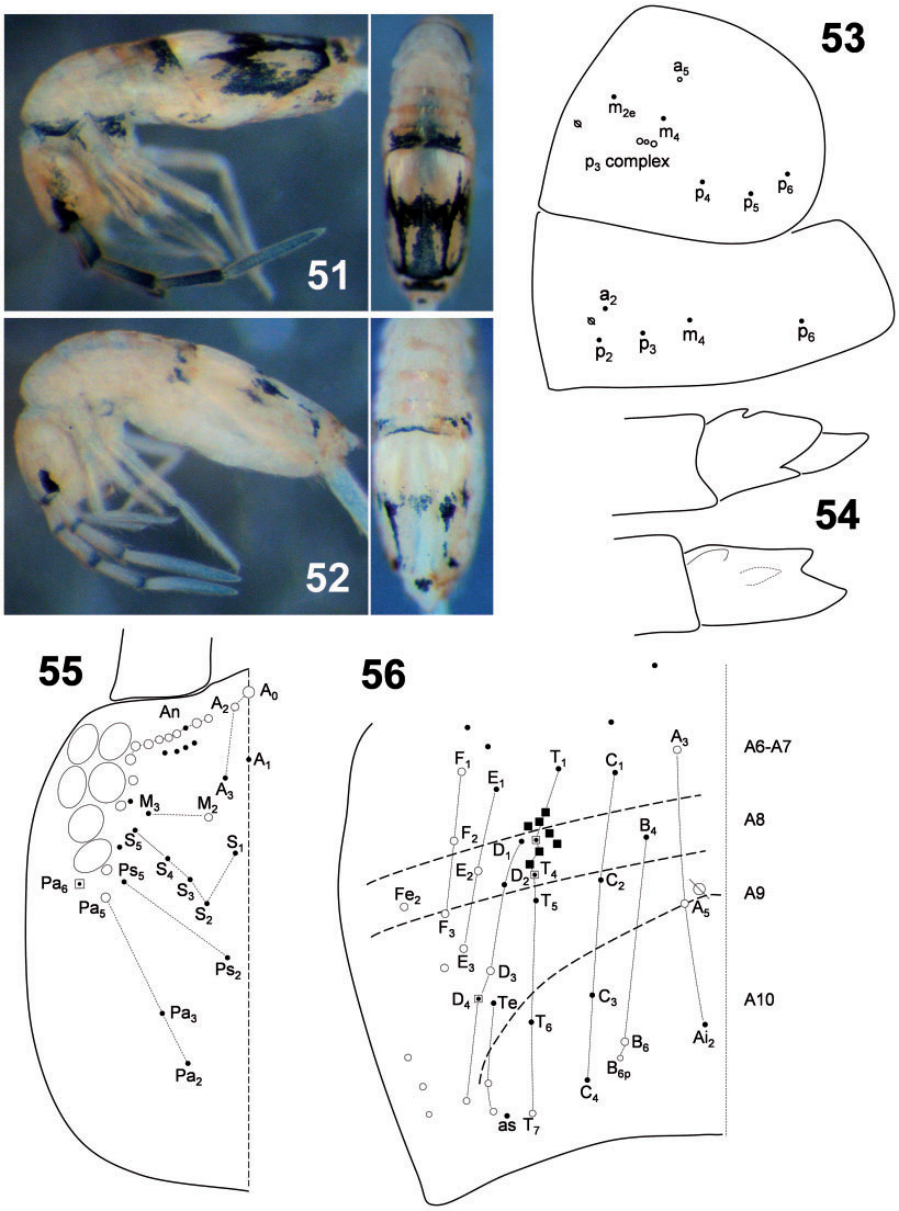


Figs. 45–50. *Trogolaphysa quisqueyana* n. sp. Open circles, macrochaetae; close circles, microchaetae; open square with dot, bothriotricha; black squares, fan-shaped setae; open circles with cross bar, pseudopores. (45) Complete dorsal chaetotaxy of fourth abdominal segment. (46) Detail of chaetae near anterior bohtriotrichal complex. (47) Lateral chaetotaxy of fourth abdominal segment in another individual. (48) Outer maxillary lobe and pleural setae. (49) Metathoracic leg claw complex. (50) Two aspects of mucro.

Eyes absent. Head dorsally (Fig. 28) with seven anterior (A_0, A_2, A_3, S_1, S_2, S_3, and S_5) and six posterior (Pa_2, Pa_3, Pa_5, Pm_3, Pp_3, and Pp_4) macrochaetae. Microchaetae distributed as in Fig. 28. Prelabral chaetae ciliate; labral chaetae smooth; distal margin of labrum smooth. Maxillary palp with subapical and papillate apical chaetae smooth; sublobal plate with 1 appendages. Lateral appendage of labial papilla E as in Fig. 29. Labial triangle with $\underline{M_1}\underline{M_2}r\underline{EL_1}l_2A_{1-5}$; M_1, M_2, E, and L_1 ciliate and subequal; r and l_2 short and smooth (Fig. 30). All postlabial chaetae ciliate. Postlabial column I with 6 chaetae, field between columns I and O with 18 chaetae (Fig. 31); ventral cervical chaetae 4+4.

Body. Dorsal body chaetotaxy as in Fig. 38. Th. II with four anterior (a_5, m_1, m_{2e}, and m_4) and six posterior (p_3 complex) macrochaetae. Posterior microchaetae normal. Th. III with four macrochaetae (a_2, p_2, p_3, and m_4); scale rounded, about 40 µm in wide (Fig. 34). Abd. I chaeta a_6 absent, with three posterior microchetae (m_3, m_4, and p_6). Abd. II with five ciliate chaetae, two macrochaetae (m_3 and m_5) and one sensillum associated with macrochaeta m_3. Abd. III with four macrochaetae (m_3, am_6, pm_6, and p_6); chaetae associated with trichobothria smooth or distally ciliate: trichobotrium a_2 with three ciliate chaetae; trichobothrium a_5 with one smooth and three ciliate anterior chaetae, trichobothrium m_5 with one ciliate anterior seta; sensillum as present, sensillum d_2 and chaeta p_5 absent. Abd. IV with two inner macrochaetae (B_4, zone 9 and B_6, zone 10) and mesochaeta B_{6p}; large lateral macrochaetae correspond to E_2, E_3, F_1, F_2, and F_3; small lateral macrochaetae as in Fig. 38; lenticular organs oval, present (3 + 3) in all specimens examined; posterior chaetae absent.

Legs. Trochanteral organ (Fig. 33) with 11 spines in "V" formation and 6 other small spines. Metathoracic claw complex as in Fig. 32. Tenent hair weakly spatulate (as in holotype), 0.5–0.8 times as long as claw. Unguis thick, with three inner teeth; paired internal teeth at 45–50% (proximal wings), basal teeth enlarged, asymmetric, longest basal tooth reaching unpaired tooth; unpaired tooth at 65–70% of inner ungual edge, almost as large as smallest of basal teeth; external and lateral teeth present. Unguiculus lanceolate, with outer margin serrated.



Figs. 51–56. *Trogolaphysa sauron* n. sp. Symbols as in previous plate. (51) Habitus of dark phase individuals. (52) Habitus of light phase individuals. (53) Dorsal chaetotaxy of thorax. (54) Two aspects of mucro. (55) Dorsal chaetotaxy of head. (56) Complete dorsal chaetotaxy of fourth abdominal segment.

Ventral Tube. Anterior face with 3+3 distal macrochaetae. Distal lateral flaps with 4 + 4 chaetae (three smooth and one ciliated distally). Posterior face with 18–19 long, coarsely ciliate chaetae.

Tenaculum. As in *Trogl. absoloni*.

Furcula. Proportion manubrium:dens:mucro length = 1:1.16:0.22. Dorsal face of manubrium with ciliate chaetae (Fig. 37). Dens tapering slightly, ventrally scaled, with a dorsal row of 13–16 smooth, stout spines with intercalated chaetae following the pattern: 4–5/$_1$/1/$_1$/1/$_1$/1/$_1$/1/$_1$/1/$_1$/1/$_1$/1–2 (chaetae in subscript), and large chaetae, becoming larger distally (Fig. 35). Mucro elongate, with three distal and two basal external subequal blunt teeth (Fig. 36).

Remarks. *Trogl. ildumensis* n. sp. belongs to the same group as *Trogl. absoloni*, in lacking eyes and having a single row of spines. Only *Troglopedetes cavernicolus* Delamare-Debouteville 1944 (Portugal), *Cyphoderopsis nepalensis* (Wilson 1982) (Nepal), *Cyphoderopsis nayakensis* (Stach 1960) (Afghanistan), *Troglopedetes pallidus* Absolon 1907 (Austria), and *Troglopedetes rasendrans* Bhattacharjee 1985 (India) have a mucro similar to the new species. The poor quality of the descriptions, by current standards, for the species listed above yield few diagnostic characters. *Trogl. ildumensis* n. sp. is similar to *C. nayakensis* and *Trogl. pallidus*, in having a relatively short mucro (dens/mucro ratio > 4), but it can be distinguished from all other member of the group by the presence of a clearly serrate unguiculus.

Genus *Trogolaphysa* Mills, 1938 sensu Thibaud and Najt, 1988

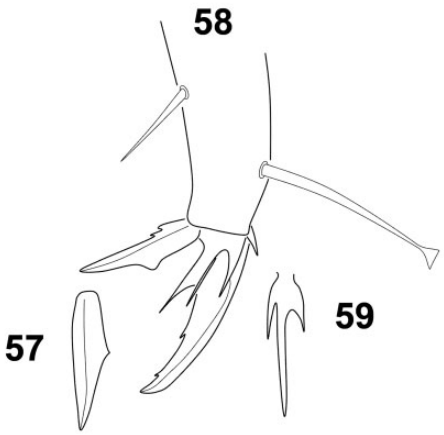
Type species *Trogolaphysa maya* Mills, 1938

Scales present on Ant I-II, head, body and ventral face of furcula; Ant IV not subdivided; eyes 0–8; labial setae L2 normal acuminate; dens with 1–2 rows of spines; mucro rectangular short or elongate, with teeth evenly distributed.

Trogolaphysa quisqueyana Soto-Adames, Jordana and Baquero n. sp.

(Figs. 39–50, Table 1)

Etymology. The epithet refers to Quisqueya, the native-American (Taino) name for the island of Hispaniola.



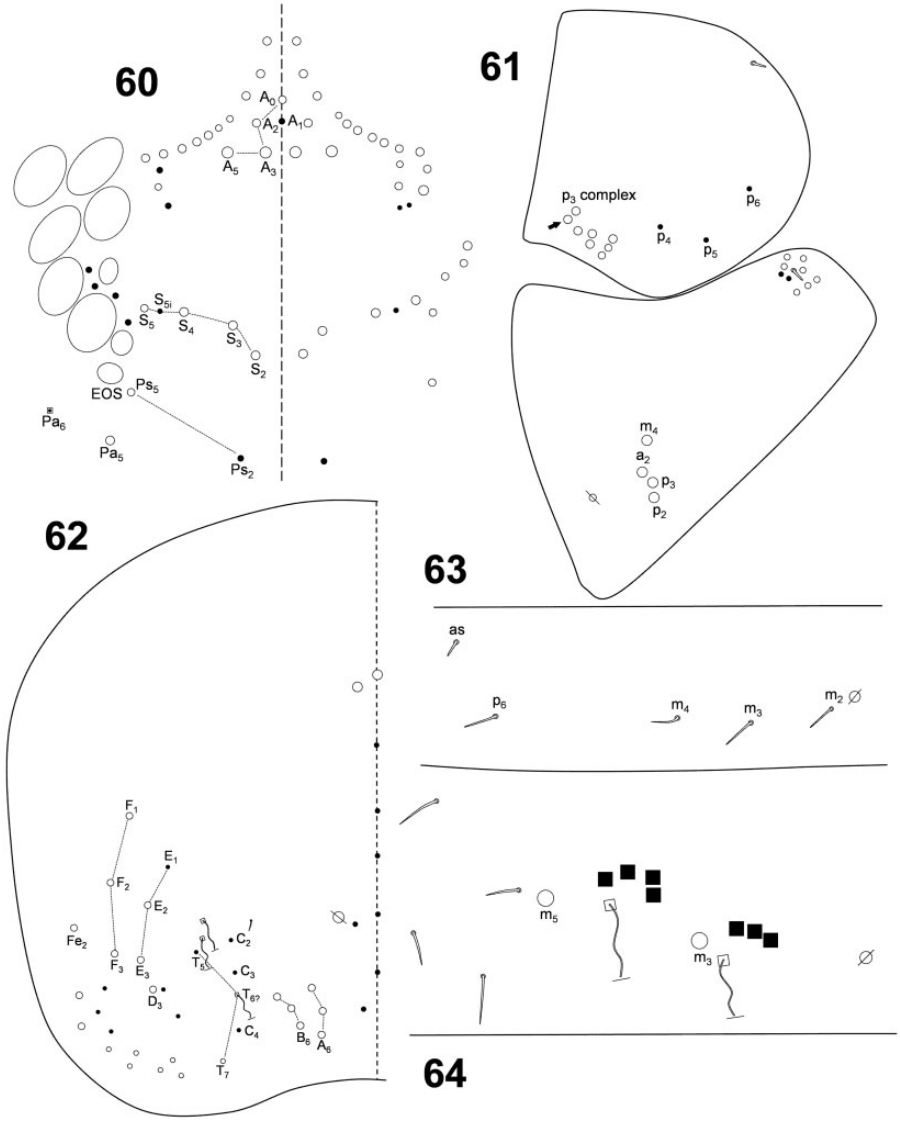
Figs. 57–59. *Trogolaphysa sauron* n. sp. (57) Unguiculus of prothoracic legs. (58) Metathoracic leg claw complex. (59) Posterior view of inner basal teeth on metathoracic legs.

Type locality. Dominican Republic: Independencia, Sierra de Bahoruco, Loma del Toro, 5.3 km SW El Aguacate, N 18.28778, W 71.71278, 2,316 m, *Pinus L.* and *Garrya Douglas* montane forest, DR43273, 29–30 March 2004, C. Young, R. Davidson, J. Rawlins. Holotype, slide mounted, deposited at CMNH.

Material Examined. Dominican Republic: Independencia, Sierra de Bahoruco, north slope, 13.5 km SE Puerto Escondido, N 18.25221, W 71.55471, 1,789 m, ecotonal *Pinus* grassland, DR41173, 24–26 March 2004, R. Davidson, J. Rawlings, C. Young, C. Núñez, M. Rial, 3 on slides, 5 in alcohol. La Vega, Cordillera Central, Valle Nuevo Station, 5.2 km ESE Valle Nuevo, N 18.78151, W 70.61192, 2,288 m, slope on open pine forest, DR23172, 23 May 2003, C. Young, J. Rawlins, C. Núñez, R. Davidson, P. Acevedo, 3 on slides. Independencia, Sierra de Bahoruco, north slope, 13.5 km SE Puerto Escondido, N 18.20907 W 71.53011, 1,807 m, broad leaf *Pinus* dens woodland, DR41273, 24–26 March 2004, R. Davidson, J. Rawlins, C. Young, C. Núñez, M. Rial, 2 on slides, 18 in alcohol. Two paratypes deposited at INHS, all other material deposited at CMNH

Size. Up to 2.2 mm.

Color Pattern. Background color creamy white (Fig. 43), brownish purple pigment uniformly distributed on antennae, mouth cone, whole



Figs. 60–64. *Campylothorax sabanus*. (60) Complete dorsal chaetotaxy of head. (61) Chaetotaxy of thorax, arrow identifies variable macrochaeta. (62) Complete chaetotaxy of fourth abdominal segment. (63) Chaetotaxy of first abdominal segment. (64) Chaetotaxy of second abdominal segment.

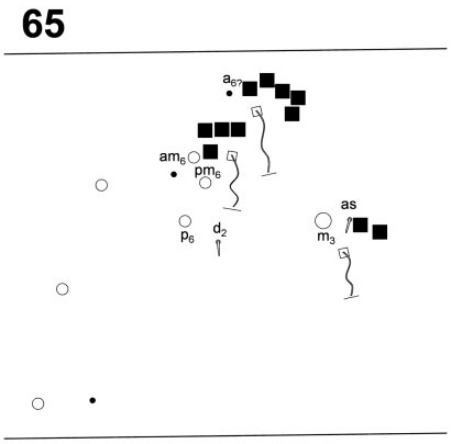


Fig. 65. *Campylothorax sabanus*. Chaetotaxy of third abdominal segment.

legs and most of Abd. 4. Pigment most intense on coxae and posterior margin of Abd. 4.

Scale Distribution. Ant. I–II and base of Ant. III, head, body, and ventral face of furcula.

Head. Antennae up to 0.60× as long as body. Ant. IV not subsegmented, with well-organized whorls of chaetae on dorsal face, ventrally whorls indistinct; subapical organ sensillum capitate; guard sensillum normal, longer and more robust than capitate sensillum; without enlarged clubbed sensilla. Sense organ of Ant. III normal rods, without additional clubbed sensilla. Eyes 8+8, eyes G and H greatly reduced, often not noticeable (Fig. 39); eye valley with 4 ciliate chaetae. Head dorsally (Fig. 40) with six anterior (A_0, A_2, A_3, M_2, S_3, and S_5) and two posterior (Pa_5 and Pm_3) macrochaetae. Microchaetae normal. Prelabral chaetae ciliate. Labral chaetae smooth. Distal margin of labrum with 1+1 small chaeta-like spines. Basal pleural chaeta coarsely ciliate, distal pleural chaeta short and smooth (Fig. 48). Maxillary palp with subapical and papillate apical chaetae smooth; sublobal plate with two appendages (Fig. 48). Labial triangle as $\underline{M_1M_2}rEL_1L_2A_{1-5}$: anterior chaetae smooth; posterior chaetae ciliate except r; chaeta r stout and smooth; L_2 slightly shorter or as long as E. All postlabial chaetae ciliate (Fig. 41); postlabial column I with four chaetae, posterior chaeta detached from others; ventral cervical chaetae 4–5+4–5; field between columns I and O with eight chaetae.

Body. Thoracic chaetotaxy as in Fig. 42. Th. II with 1 anterior (a_5) and six posterior (p_3 complex) macrochaetae; Th. III without macrochaetae. Thoracic microchaetae normal. Abd. I with chaeta a_6 absent in all but one individual examined; with four posterior microchaetae present (m_2, m_3, m_4, and p_6). Abd. II with two macrochaetae (m_3 and m_5) and one sensillum associated with macrochaeta m_3; trichobothrium m_2 and a_5 with three and 4–5 anterior fan-shaped supplementary microchaetae, respectively; microchaeta a_6 and m_6 ciliate, acuminate; p_5 ciliate fusiform. Abd. III with four macrochaetae (m_3, am_6, pm_6, and p_6); microchaetae associated with trichobothrium complexes fan-shaped; trichobothrium m_2 with two anterior chaetae, trichobothrium a_5 with six anterior chaetae, trichobothrium m_5 with three anterior chaeta; sensilla as and d_2 present; additional ciliate chaetae external to lateral trichobothrial complex arranged as in other *Trogolaphysa* for which lateral chaetotaxy is known (e.g., Soto-Adames and Taylor 2013, Fig. 16). Abd. IV (Fig. 44) with four inner macrochaetae (A_3, zones 6–7; A_5, zone 10; B_5, zone 9; B_6, zone 10), mesochaeta B_{6p} present. Detail of anterior trichobothrial complex as in Fig. 46. Anterior chaeta on column Te either a microchaeta (Fig. 45) or a macrochaetae (Fig. 47), posterior chaeta always a small macrochaeta; large lateral macrochaetae correspond to D_3, E_2, E_3, F_1, F_2, and F_3, small lateral macrochaetae as in Figs. 45 and 47; posterior chaetae 12–14; lenticular organs apparently 5–7 but unclear in all specimens examined.

Legs. Trochanteral organ with up to 28 spine-like chaetae. Metathoracic claw complex as in Fig. 49. Tenent hair spatulate, proportion inner edge of claw: tenent hair = 0.83. Smooth posterior chaetae on metathoracic legs 0.83× (0.78–0.87) as long as unguiculus. Unguis with four inner teeth: basal teeth asymmetric, one larger, larger basal tooth inserted at 43% of inner ungual edge; proximal unpaired tooth shorter than basal paired teeth, inserted at 67% of inner edge; distal unpaired tooth smallest of all inner teeth, inserted at 85% of inner edge. Outer tooth ending on basal quarter of outer ungual edge. Unguiculus lanceolate, with outer margin smooth.

Ventral Tube. Anterior face with 2+2 distal macrochaetae, other chaetae not seen.

Tenaculum. As in *Trogl. absoloni*

Furcula. Proportion manubrium:dens:mucro length = 1:1:0.07 ($n = 7$).

Dens with 2 rows of ciliate spines: inner row with 35–42 spines; outer row with 25–28 spines. Mucro with four short, stout teeth (Fig. 50), basal outer tooth reaching to at least half the length of basal inner tooth; mucro 3.1–3.5× as long as width of dens tip.

Remarks. *T. quisqueyana* n. sp. is unique among species with 6–8 eyes and spatulate tenent hair in having six anterior dorsal head macrochaeta, four chaetae in eye valley, and outer and lateral ungual teeth ending on basal fourth of outer margin. Among species for which the dorsal chaetotaxy is known, the new species is most similar to *Trogolaphysa riopedrensis* (Mari Mutt 1987), from which it can be distinguished by the characters listed above, and by having the basal mucronal teeth almost aligned instead of sequential.

Trogolaphysa carpenteri (Denis 1925), *Trogolaphysa berlandi* (Denis 1925), *Trogolaphysa separata* (Denis 1933), *Trogolaphysa distinguenda* (Denis 1931), and *Trogolaphysa hirtipes* (Handschin 1924) have been reported as having 6–8 eyes and spatulate tenent hair, but they are otherwise so poorly described by current standards that separation from the new species is provisional. *T. carpenteri* seems to differ from the new species in having only three inner teeth on the unguis and, if Yoshii's (1988) material from Mexico actually represents *T. carpenteri*, by having only two anterior dorsal head macrochaetae (A_0 and A_2) and lacking mesothoracic macrochaetae. *Trogolaphysa berlandi* has only one row of dental spines; *T. separata* has the outer and lateral teeth of the unguis inserted on the distal half the dorsal margin, whereas *T. hirtipes* has the basal ungual teeth inserted near the basal quarter of the claw and the manubrium ostensibly longer than the dens.

Trogolaphysa sauron Soto-Adames, Jordana and Baquero n. sp.
(Figs. 51–59, Table 1)

Etymology. Refers to the resemblance of the dorsal pattern on the fourth abdominal segment with the helmet of Sauron, the character in Lord of the Rings, as represented in Peter Jackson's 2001 film.

Type Material. Martinique: Plateau Concorde, primary forest of chestnut and white gum, 680 m on dead logs, sample M.153, 23 February 1981, J-M. Thibaud and Z. Massoud. Holotype, slide mounted, deposited at the MNHN.

Material Examined. Martinique: same as holotype, 3 on slides, and 40 (mostly small juveniles) in alcohol. Two paratypes deposited at INHS, all other material deposited at MNHN.

Size. Up to 1.9 mm.

Color Pattern. Background color light yellow to white, purple pigment distributed according to two general patterns, one dark, one light (Figs. 51 and 52). Pattern in light individuals clearly representing a subset of pattern in dark individuals and not a fundamentally different pattern.

Scale Distribution. Ant. I–II and base of Ant. III, head, body, and ventral face of furcula.

Head. Antennae up to 0.66× as long as body. Ant. IV not subsegmented, with well-organized whorls of chaetae on dorsal face, ventrally whorls indistinct; subapical organ inserted very close to tip of segment, sensillum capitate, but small, almost without pedicel, and translucent, seemingly absent in most mounted specimens; guard sensillum apically

constricted. Sense organ of Ant. III normal rods. Eyes 8+8, but appearing as 6+6 (Fig. 55), eyes G and H greatly reduced and often not visible, even at high magnification; eye valley with 4 ciliate chaetae, as in *T. quisqueyana* (Fig. 39). EOS not seen. Head dorsally (Fig. 55) with three anterior (A_0, A_2, and M_2) and one posterior (Pa_5) macrochaetae. Prelabral chaetae ciliate. Labral chaetae smooth. Distal margin of labrum with 1+1 small seta-like spines. Basal pleural chaeta coarsely ciliate, distal pleural chaetae short and smooth as in *T. quisqueyana* n. sp (Fig. 48). Maxillary palp with subapical and papillate apical chaetae smooth; sublobal plate with two appendages. Labial triangle as $\underline{M_1M_2}rE\underline{L_1L_2}A_{1-5}$: anterior chaetae smooth; all posterior chaetae, except r, ciliate; r stout and smooth as in *Trogl. absoloni* (Fig. 9); L_2 as long as or slightly shorter than E. All postlabial chaetae ciliate. Postlabial column I with four chaetae, ventral cervical chaetae four; with eight chaetae in field between columns I and O.

Body. Thoracic chaetotaxy as in Fig. 53: Th. II with one anterior (a_5) and three posterior (p_3 complex) macrochaetae; Th. III without macrochaetae. Abd. I chaeta a_6 present; four posterior microchaetae present (m_2, m_3, m_4, and p_6). Abd. II with two macrochaetae (m_3 and m_5) and one sensillum associated with macrochaeta m_3; trichobothria m_2 and a_5 with 3 and 4–5 fan-shaped supplementary microchaetae, respectively; microchaetae a_6 and m_6 acuminate, ciliate; p_5 fusiform, ciliate. Abd. III with four macrochaetae (m_3, am_6, pm_6, and p_6); microchaetae associated with trichobothrial complexes fan shaped; trichobothrium m_2 with two anterior chaetae, trichobothrium a_5 with six anterior chaetae, trichobothrium m_5 with three anterior seta; sensilla as and d_2 present; additional ciliate chaetae external to lateral trichobothrial complex arranged as is typical for *Trogolaphysa* (cf. Soto-Adames and Taylor 2013, Fig. 16).

Abd. IV (Fig. 56) with three inner macrochaetae (A_3, zones 6–7, A_5, zone 9; B_6, zone 10) mesochaeta B_{6p} present; column Te with 1 micro- and 1–2 macrochaeta; large lateral macrochaetae correspond to D_3, E_2, E_3, F_1, F_2, and F_3; small lateral macrochaetae as in Fig. 56; posterior chaetae 13–14; lenticular organs apparently 4, but unclear in all specimens examined.

Male Genital Plate. Circinate, as in *Trogl. absoloni*.

Legs. Trochanteral organ with up to 24 spine-like chaetae. Metathoracic claw complex as in Fig. 58. Tenent hair spatulate, proportion inner edge of claw: tenent hair = 1.0.

Unguis with four inner teeth: basal teeth asymmetric, one tooth longer and more slender than other (Fig. 59), longest tooth inserted at 25% of inner ungual edge; unpaired teeth minute and subequal, proximal unpaired tooth often present as a simple mound, without a discernible tooth; proximal unpaired tooth inserted at 51% of inner edge, distal unpaired tooth inserted at 84% of inner edge. Outer tooth ending on basal quarter of outer ungual edge, lateral teeth ending on basal half. Unguiculus truncate (Fig. 57), outer margin smooth or with 2–3 small teeth, inner margin with one tooth.

Ventral Tube. Anterior face with 3+3 distal macrochaetae, other chaetae not seen.

Tenaculum. As in *Trogl. absoloni*.

Furcula. Proportion manubrium:dens:mucro length = 1:1:0.07 ($n = 3$). Dens with 2 rows of ciliate spines: inner row with 32–38 spines; outer row with 20–23 spines. Mucro with 4 short, stout teeth (Fig. 54), mucro 2× as long as width of dens tip.

Remarks. *T. sauron* n. sp. can be distinguished from all other members of the genus by its unique color pattern and combined presence of a truncate unguiculus, three mesothoracic macrochaetae, and needle-shaped paired ungual teeth. Among species with known chaetotaxy only *T. jacobyi*, *T. belizeana*, *Trogolaphysa bessoni* Thibaud and Najt 1989 and *Trogolaphysa cotopaxiana* Thibaud and Najt 1989 have three posterior macrochaetae on Th. II: the first three species are troglomorphs, with acuminate tenent hair and without eyes or pigment, whereas *T. cotopaxiana* is white, without pattern, has a single row of dental spines, a five-toothed mucro and small fin-like inner ungual teeth. Among species for which the chaetotaxy is unknown, *Trogolaphysa sauron* n. sp. is similar to *Trogolaphysa haitica* (Palacios-Vargas et al. 1985), in having needle-shaped inner ungual teeth, but the two species differ in almost all other general morphological characters. *Trogolaphysa millsi* Arlé 1939 and *Trogolaphysa tijucana* Arlé and Guimarães 1979 are the only other members of the genus with truncante unguiculus, but they differ from *T. sauron* n. sp. in color pattern, in having only two eyes and in that the paired ungual teeth are fin shaped.

Dorsal Chaetotaxy of *Troglopedetes, Trogolaphysa*, and *Campylothorax*. The discussion that follows is based on observations of species described above (Table 1), those described by Soto-Adames and Taylor (2013), and when possible, Deharveng (1987, 1988, 1990), and Deharveng and Gers (1993). Mitra and Dallai (1980) and Mitra (1993, 2002) present drawings for *Campylothorax* and *Trogolaphysa*, but these data were not incorporated because the stylized drawings make it difficult to determine homologies, even in comparisons with *C. sabanus* and *T. jataca*. In the descriptions below, we first identify conserved elements followed by elements unique to each genus.

Head (Figs. 11, 28, 55, and 60). When compared with other scaled Entomobryioidea, the three genera have a reduced chaetotaxy. All species lack chaetae M_0, S_0, but most characteristically, Ps_3 is also absent. The dorsal chaetotaxy of the head has the same organization in *Trogolaphysa* and *Troglopedetes*, whereas in *Campylothorax,* some aspects of the organization of elements in series A are different.

In the three genera, chaeta A_1 is always an acuminate, coarsely ciliate microchaeta, but all other members of the series can develop into macrochaetae. In *Trogolaphysa* and *Troglopedetes,* chaetae A_1 and A_3 are inserted well posterior to A_0 and A_2, more or less in line with the most posterior chaetae in row An, whereas in *Campylothorax,* chaetae A_{0-3} form a compact group near the point of inflection of row An (cf. Figs. 11, 55, and 60). *Campylothorax* has 1+1 macrochaetae external to A_3 that could be interpreted as either A_4 or A_5. *Trogolaphysa* and *Troglopedetes* also have microchaetae that can be interpreted as A_4 or A_5, whereas in *Troglopedetes,* these chaetae appear to be stable and identifiable, and in *Trogolaphysa* they are unstable, varying between individuals and asymmetrically within individuals.

In *Trogolaphysa* and *Troglopedetes,* series M includes up to two chaetae here considered homologous to M_{2-3}. Chaeta M_2 is often developed into a macrochaeta. Series M is absent in *Campylothorax*.

All species have at least four posterior chaetae in series S (S_{2-5}). *Trogolaphysa* and *Troglopedetes* also carry anterior chaeta S_1, which is absent in *C. sabanus* (Fig. 60), but lack chaeta S_{5i}, which is present in that species. The pattern of macrochaetae differs in the three genera. In *Trogolaphysa,* only S_3 and S_5 are transformed into macrochaetae, and in *Troglopedetes* S_1, S_2, S_3, S_4 (some species from Thailand only), and S_5 can be macrochaetae, whereas in *Campylothorax,* all posterior members of the series, except S_{5i}, are transformed into macrochaetae. Microchaeta S_{5i} in *C. sabanus* may represent a posteriorly displaced M_3.

Series Ps of all species considered here includes chaetae Ps_2 and Ps_5, whereas Ps_3 is absent. Row Pa in *Trogolaphysa* and *Troglopedetes* includes chaetae Pa_2, Pa_3, Pa_5, and Pa_6, but in *Campylothorax,* only macrochaetae Pa_5 and bothriotrix Pa_6 remain. Pa_2 and Pa_3 are macrochaetae in all *Troglopedetes* but microchaetae in *Trogolaphysa*. Chaeta Pm_3 is the only member of row Pm present in *Trogolaphysa* and *Troglopedetes*, and it is often transformed into a macrochaeta in both genera. The number of chaetae in row Pp is unclear, but Pp_3 appears to be a microchaetae in *Trogolaphysa* and a macrochaetae in *Troglopedetes*.

Mesothorax (Figs. 22, 38, 42, 53, and 61). Only chaetae p_{4-6} are conserved in the same general spatial distribution in the three genera. In *Trogolaphysa* and *Troglopedetes,* the homology of chaetae a_5, m_{2e} m_4, and the p_3 complex seems uncontroversial. In the species studied, p_3 forms a complex of either three or six macrochaetae, similarly arranged in both genera, and p_{1-2} appears to be absent. It is likely that the p_3 complex includes p_{1-3}. The six macrochaetae could be explained by a duplication of p_{1-3} (as p_1, p_{1i}, p_2, p_{2i} p_3, and p_{3i}). The presence of

microchaetae $p_{1–2}$ in *Trogolaphysa giordanoae*, which has six macrochaetae in the p_3 complex, seems to invalidate the previous conclusion. However, Soto-Adames and Taylor (2013) have suggested that microchaetae that $p_{1–2}$ in *T. giordanoae* is secondary. Clarification of the homology of these chaetae requires further analysis. In *C. sabanus* (Fig. 61), the inner posterior complex includes seven (rarely eight) macrochaetae in a peculiar arrangement and their homology is uncertain. Assuming that the chaetae conserved in *Trogolaphysa* and *Troglopedetes* are also conserved in *C. sabanus*, it is possible that the inner macrochaetae in the posterior complex comprise six chaetae in the p_3 complex plus a posteriorly displaced m_{2e}.

Unique conditions of the mesothoracic chaetotaxy include the presence in *Troglopedetes* from Spain of chaeta m_1, transformed into a macrochaeta associated with the mesothoracic collar; presence of m_{2i} in *T. jacobyi*; and absence of a_5 and m_4 in *C. sabanus*.

Metathorax (Figs. 22, 38, 42, 53, and 61). The chaetotaxy of the three genera is considerably reduced. All species have only four inner posteromedial chaetae, but their relative insertion varies according to whether they are micro- or macrochaetae, and the real identity of the elements is unclear. Following Soto-Adames and Taylor (2013), in species like *T. quisqueyana* n. sp. and *T. sauron* n. sp., which carry only microchaetae, the chaetae appear to correspond to a_2, p_2, p_3, and m_4 (Fig. 43). This arrangement is retained when only one chaeta (usually p_3) is transformed into a macrochaeta. When three inner chaetae are macrochaetae, as in the two species of *Troglopedetes*, *T. giordanoae* and *T. belizeana*, the two posterior chaetae move closer together and the anterior migrates posteriorly to form a triangle (Fig. 22). In *Troglopedetes*, the triangular pattern is retained even when putative m_4 is transformed into a macrochaeta. *Campylothorax* (Fig. 61) carries four macrochaetae, but they are arranged into a column. The identification of macrochaetae in *C. sabanus* is suggested by the arrangement of macrochaetae in *Trogl. ildumensis* n. sp. (Fig. 38).

A lateral posterior chaeta is present in *Trogl. absoloni* and all *Trogolaphysa* studied. This chaeta is absent in *Trogl. ildumensis* n. sp. and *C. sabanus*.

First Abdominal Segment (Figs. 22, 38, and 63). The chaetotaxy of this segment is reduced to such extent that the identity of the chaetae is a matter of speculation. All species have three posterior chaetae probably homologous to m_3, m_4, and p_6. Most species, including *C. sabanus*, also have m_2 (Fig. 63). Most species of *Trogolaphysa* also have a_6 inserted near the lateral microsensillum (Fig. 59 in Soto-Adames and Taylor 2013).

Second Abdominal Segment (Figs. 22, 38, and 64). The chaetotaxy of this segment is also considerably reduced. The chaetae associated to trichobothrium m_2 are the same in the three genera, but the chaetae external to trichobothrium a_5 differ. Chaetae a_3, m_{3e}, p_4, and m_4 are absent. Chaetae associated with m_2 are 2–3 fan-shaped or ciliate supplementary chaetae, sensillum as and macrochaeta m_3. The chaetae associated to trichobothrium a_5 are the 2–4 anterior supplementary fan-shaped chaetae and macrochaeta m_5. In all *Trogolaphysa* and *Trogl. absoloni* (Fig. 22), the chaetae external to a_5 are a_6, m_6, and p_5, but in *Trogl. ildumensis* n. sp. (Fig. 38) and *C. sabanus* (Fig. 64), homologies are unclear.

Third Abdominal Segment (Figs. 22, 38, and 65). All species have the same chaetotaxy: trichobothrium a_2 complex has two fan-shaped supplementary chaetae, sensillum as and macrochaeta m_3; trichobothria a_5 and m_5 complex have 4–9 fan-shaped supplementary chaetae and three latero-posterior macrochaetae. All species, except *T. jacobyi*, have sensillum d_2 inserted at the level of the middle macrochaeta. There are two other columns of chaetae of uncertain homology lateral to the macrochaetae; the inner column includes three microchaetae in *Trogolaphysa* and *Troglopedetes* and two in *C. sabanus* (Fig. 65), the outer column includes three meso- or small macrochaetae in all species.

Fourth Abdominal Segment (Figs. 22, 38, 44, 56, and 62). The chaetotaxy of Abd. 4 includes three (A, B, and C) more or less organized columns internal to the bothriotrichal complex (column T) and three (D, E, and F) columns external to the complex. Common elements to the three genera are the presence of macrochaetae B_6, D_3, E_2, E_3, F_1, and F_2. *Trogolaphysa* and *Troglopedetes* share secondary posterior mesochaeta B_{6p}, and secondary trichobothrium D_4. *Campylothorax* (Fig. 62) lacks chaeta B_{6p} and the secondary trichobothrium appears homologous to T_6. In addition, *C. sabanus* differs from *Trogolaphysa* and *Troglopedetes* in having a column of, presumably, secondary chaetae running along the middle of the segment, ending anteriorly on the medial unpaired macrochaeta, and in having all macrochaetae in columns A and B displaced toward the posterior margin of the segment and inserted in zone 10.

In *Troglopedetes* and *Trogolaphysa,* the determination of the actual number of normal microchaetae in the central area of the segment (area between bothriotrichal complexes) is difficult. The central area carries many sensilla-like chaetae with sockets indistinguishable from those of normal chaeta, and without the shaft, it is usually impossible to categorize the organ. Most sensilla are inserted near a scale, whereas chaetae are not, but this is not always the case. This problem is particularly acute in zone 7, where microchaetae are very short and their placement seems to be determined by the anterior elongation of the segment in each species.

Inner columns A, B, and C comprise 3–4, 2–4, and 4 chaetae, respectively, whereas in each of the three external columns (D, E, and F), only the three anterior elements can be unambiguously identified. Most of the variation in the number of chaetae in columns A and B is attributable to the troglomorphic species. All surface species and *T. giordanoae* (collected in a cave but not troglomorphic) have three chaetae in columns A and B, whereas the two troglomorphic *Trogolaphysa* from Belize have 3, 2 chaetae and the *Troglopedetes* from Spain have 3, 4, and 4, 3 chaetae.

Most inner chaetae in *Trogolaphysa* and *Troglopedetes* show considerable lateral and antero-posterior displacement in interspecific comparisons. There is a trend in members of these two genera for chaetae to be displaced toward the posterior margin of the segment. This trend is most evident in *Trogolaphysa*, where, e.g., A_5 is a macrochaeta inserted in zone 10, whereas in the two species of *Troglopedetes*, A_5 is a microchaeta inserted in zone 9.

Discussion

Homology and Nomenclature of Chaetotaxy in *Troglopedetes*, *Trogolaphysa*, and *Campylothorax*. Nomenclature systems developed by Szeptycki (1979) and Soto-Adames (2008) for head and body chaetotaxy of Entomobryidae were predicated on the basis of putative homology of the elements, as determined by studies of the postembryonic development. Three factors confuse homology determination of individual elements: plurichaetosis, extreme reduction in element number, or extensive insertion displacement. It is evident that the nomenclature systems become difficult to apply as the number of chaetae departs in either direction from the number found in the first instar. As the number of elements of the idiochaetotaxy increases, the insertion of each individual chaeta is displaced until it becomes impossible to identify basic elements. This is the condition found in most genera lacking scales such as those in tribes Orchesellini, Entomobryini, Cremastocephalini, and Callyntrurini (e.g., Mari Mutt 1979, Mitra 1993, Potapov and Kremenitsa 2008, Jordana 2012). At the other extreme are species with dense scale cover and such reductions in idiochaetotaxy of some segments that appropriate landmarks are lacking to identify the elements that remain. This is evident in the genera *Trogolaphysa*, *Troglopedetes,* and *Campylothorax* and in some Lepidocyrtini (*Metasinella*, some *Pseudosinella*, Mari Mutt and Gruia 1983, Mari Mutt 1986, Soto-Adames 2002), some *Lepidosira* (Seirini, F.N.S.A., unpublished data), and *Cyphoderus* (Cyphoderini, Szeptycki 1979). Displacement of individual elements introduces ambiguity in homology determination because it is unclear if the displaced element represents precisely that or if it represents a secondary chaeta sprouted during postembryonic development.

In the genera of Paronellidae considered here, ambiguity in homology determination is brought about by extreme reduction and displacement of idiochaetotaxy. The effect of the interaction between these factors is most evident on the inner fields of the meso- and metathorax, and first and fourth abdominal segments. The inner chaetotaxy of the second and third abdominal segments is reduced to such extent that there is little to homologize. The number of chaetae is greatly reduced in all species, and when transformed into macrochaetae, individual elements are displaced to form clusters.

The chaetotaxy of the fourth abdominal segment is particularly interesting, as some elements seem to be missing in some species, whereas others are displaced along longitudinal and transversal tracks in interspecific comparisons. Soto-Adames and Taylor (2013) assumed that fourth abdominal segment inner secondary chaetae are rare and considered the eight posterior chaetae in columns A and B to be primary. Based on these assumptions, Soto-Adames and Taylor (2013) named chaetae sequentially, from posterior to anterior, irrespective of relative insertion position. This study follows Jordana and Baquero (2005) and Jordana (2012) in assuming that secondary chaetae are common and homology is determined by insertion location not by simple sequence in a series. Determination of which of these two systems more faithfully reflects the evolution of chaetotaxy in Paronellidae and Entomobryidae will require additional analysis. Diptera taxonomists have dealt with problems of homology determination by studying patterns of chaeta nerve connection changes during postembryonic development (Belkin 1960, Harbach 1991, Craig 2005). Research on patterns of nerve connections may also prove valuable to reach consensus on a nomenclature system for entomobryoid springtails. However, irrespective of whether the homology of individual chaetotaxy elements can be established unambiguously, their diagnostic value is unquestionable. The current lack of nomenclature consensus makes evident that descriptions referring to chaetae by name only are incomplete if not accompanied by illustrations displaying the precise spatial organization of the chaetae.

***Troglopedetes* and *Trogolaphysa* Have the Same Chaetotaxy Organization.** The distinction between *Trogolaphysa* and *Troglopedetes* hinges on the presence or absence of a medial division on the fourth antennal segment and mucro morphology (Thibaud and Najt 1988). It was suggested (Mitra 1993, Soto-Adames and Taylor 2013) that chaetotaxy could provide additional diagnostic characters to separate these genera, but the data presented here indicate otherwise. Neither the number of chaetae nor the pattern of body macrochaeta shows diagnostic differences between the genera. Only the presence of head macrochaetae Pa_2 and Pa_3 in *Troglopedetes* and their absence in *Trogolaphysa* appears to be diagnostic, but this observation needs to be confirmed by examination of more species from each genus.

Troglopedetini Is a Junior Synonym of Paronellini. Genera in subfamily Paronellinae have been grouped into five tribes, in part based on common aspects of the chaetotaxy (Mitra 1993). Members of tribe Cremastocephalini differ from all other Paronellinae in not having scales, members of Callyntrurini have fusiform scales and abundant macrochaetotaxy, whereas members of Bromacanthini, Paronellini, and Troglopedetini have rounded scales and reduced or no macrochaetotaxy. The tribe Bromocanthini is an amalgam of seemingly unrelated genera and probably will not withstand detailed phylogenetic scrutiny (Mitra 1993). Paronellini and Troglopedetini, on the other hand, form a homogeneous group where even generic diagnoses have been, until recently, unclear (Thibaud and Najt 1988, Soto-Adames and Taylor 2013).

Soto-Adames et al. (2008) included seven genera in Troglopedetini, but three genera have been synonymized: Thibaud and Najt (1988) synonymized *Dicranocentruga* with *Trogolaphysa* and *Trichorypha* with *Paronella*, whereas Deharveng and Bedos (1995) synonymized *Microparonella* Carpenter with *Troglopedetes*. These nomenclatorial acts leave only *Troglopedetes*, *Trogolaphysa*, *Cyphoderopsis,* and *Troglobius* Palacios-Vargas and Wilson 1990, assigned to Troglopedetini. *Troglobius* is a small genus of cave-adapted species with uncertain phylogenetic affinities, characterized by a peculiar mucro and absence of spines on dens. Tribe assignment for *Troglobius* will have to await detailed description of the dorsal chaetotaxy of the species[4]. The other three genera assigned to Troglopedetini sensu Mitra (1993) harbor *Paronella*-like species with reduced eyes number, many of which are troglomorphic, whereas the three genera in tribe Paronellini sensu Mitra (1993) include species with 6–8 eyes most of which live in surface habitats and lack adaptations to subterranean life. Analysis of species in these tribes (Soto-Adames and Taylor 2013) suggests that Trogopedetini represents a group of specialized forms related to species in Paronellini, the same way *Pseudosinella Shäffer* relates to *Lepidocyrtus Bourlet* or *Sinella Brook* to *Entomobrya Rondani* (Yoshii, 1988).

Evidently, separation of *Troglopedetes* and *Trogolaphysa* in two different tribes is unnecessary and makes Troglopedetini polyphyletic. The synonymization of *Dicranocentruga* with *Trogolaphysa* (Thibaud and Najt 1988) based on characters of the antennae and furcula was the first step in the fusion of the tribes. Soto-Adames and Taylor (2013) provided additional evidence for the synonymy of *Dicranocentruga* and *Trogolaphysa* by showing that species assigned to both genera have EOS and identical chaetotaxy organization. Jantarit et al. (2013) have also shown that the organization and level of reduction of the chaetotaxy in *Cyphoderopsis* is almost identical to that in *Trogolaphysa*. The analysis presented here adds evidence in support of a common origin and close relationship between *Troglopedetes, Trogolaphysa,* and *Cyphoderopsis* by highlighting the similarity in chaetotaxy organization in these three genera when compared with *Campylothorax*.

On the basis of the evidence presented above, we propose the synonymization of Troglopedetini and Paronellini, with a new circumscription of Paronellini as follows:

Diagnosis of Paronellini. Paronellidae with 0–8 eyes, basic chaetotaxy composed of hyaline, denticulate, apically rounded scales present dorsally on head, body, and ventrally on manubrium and dens; idiochaetotaxy reduced, head chaeta Ps_3 absent, metathorax with four inner chaetae, first abdominal segment with 2–3 inner chaetae; second and third abdominal segments each with one inner macrochaetae and one inner sensillum, without inner microchaetae in addition to supplementary chaetae associated with trichobothria; fourth abdominal segment with three trichobothria.

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[4] While this article was in press, Zeppellini et al. (2014) transferred the genus *Troglobius* to subfamily Cyphoderinae.

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